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Environmental and ammonoid faunal changes related to Albian Bay of Biscay opening: Insights from the northern margin of the Basque-Cantabrian Basin

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ABSTRACT

The opening and ocean floor spreading of the Bay of Biscay began in the earliest Albian. The integrative study of the Albian sedimentary record and its ammonoid fauna (around 250 specimens) from the northern margin of the Basque-Cantabrian Basin indicates that environmental changes, occurred as a consequence of the Bay of Biscay opening, triggered significant ammonoid bioevents. Main bioevents are diversity changes in the ammonoid associations, occurrence of large forms (diameter up to 0.45 m) and the incursion of elements from other basins. Time-correlation of faulting pulses with ammonoid bioevents indicates that transtensive tectonics was ultimately the major control on the marine environmental conditions such as depth, sea bottom physiography, seaways, sedimentary systems and sea-water chemistry. The pulsating faulting during the Albian led to the increment of the subsidence rate, the deepening and widening of the margin and the progressive increase in the oceanic circulation between the margin and the nascent Bay of Biscay and North Atlantic. In addition, Albian synsedimentary faults constituted conduits for ascending magmas and hydrocarbon-rich hydrothermal fluids, which expelled to the seafloor, causing changes in the sediments, the sea-water chemistry (fertilization) and biota. The integration of sedimentological and palaeontological data has given the basis for a conceptual model of the ammonoid habitats.

1. Introduction

Mesozoic rocks deposited in the northern margin of the Basque Cantabrian Basin (BCB) record rifting processes that led to the opening of the Bay of Biscay (Rat, 1988). During the Albian, and coeval to the beginning of the seafloor spreading in the western part of the Bay of Biscay, hyperextension of the crust caused faulting, maximum subsidence and deepening of the margin (Jammes et al., 2009). This allowed for the deposition of a thick succession of deep-water sediments, i.e. the Black Flysch Group, which host a rich and diverse fauna of ammonoids. Besides the biostratigraphical value of these ammonoid associations, which have been the basis for timing the otherwise difficult to date the thick and facies-changing sedimentary successions, their value to understand the environmental conditions and changes in a deepening marine basin are of key interest.

In the last years, ammonoid habitats have been inferred from the study of the conch parameters and hydrodynamic characteristics (e. g., Westermann, 1996) and from the relationship to the sedimentary facies (e. g., Batt, 1993). Recently, new evaluations of the morphology (e. g., Ritterbush and Bottjer, 2012) and the use of stable isotope analysis of

the conch (Lukeneder et al., 2010), in addition to new advances in their palaeobiology, have permitted to better understand the environments inhabited by ammonoids (e. g., Lukeneder, 2015). Based on collected ammonoids, this study establishes an Albian biozonation for the entire northern margin of the Basque Cantabrian Basin, distinguishes several local bioevents and addresses the response of the ammonoid fauna to environmental changes inferred from the accurately studied Albian sedimentary record. The integration of these sedimentological and palaeontological data is the basis for the construction of a conceptual model of the ammonoid habitats which provides an improved understanding on the environments in which they thrived and on the environmental changes in a fastly evolving margin of the Bay of Biscay.

2. Geological and palaeontological background

The studied Albian sedimentary rocks and their ammonoid fauna belong to the northern margin of the Basque-Cantabrian Basin (BCB), a Mesozoic peri-cratonic rift basin related to the opening of the North Atlantic and the Bay of Biscay (Fig. 1). The Bay of Biscay is a V-shaped oceanic embayment widened toward the west, formed between Early

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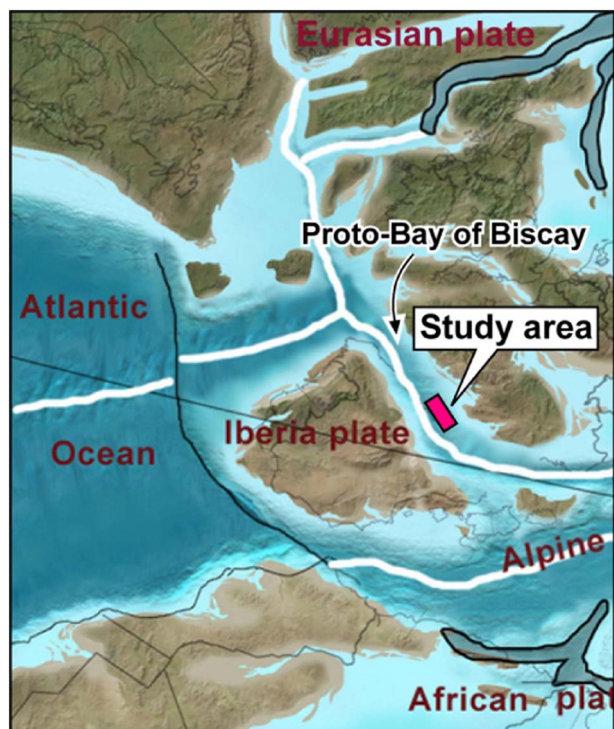


Fig. 1. Albian (100 Ma) palaeogeographic map of the North Atlantic showing the nascent Bay of Biscay between Iberia and Laurasia plates. The studied northern margin of the BCB is indicated.

Source: <http://cpgeosystems.com>.

Albian and Santonian times (Montadert et al., 1974). The oceanic floor spreading led to the anticlockwise rotation of the Iberian plate by 35–37° with respect to Eurasia and the opening of the Bay of Biscay (Van der Voo, 1969). In the front of this propagating ocean three main Mesozoic rift basins, i.e. Basque-Cantabrian, Parentis and Maule-Arzacq basins, were formed (Vergés et al., 2001). These basins experienced an Albian phase of maximum extension and subsidence coincident with the initiation of the sea floor spreading in the Bay of Biscay (Brunet, 1994). Recent works interpret these basins as magma-poor hyperextended rifts characterized by extremely thinned crust and locally also exhumed mantle (Jammes et al., 2009), but without oceanization. Cenozoic inversion of the BCB led to intense folding and thrusting of their sedimentary records (Vergés et al., 2001).

The Cretaceous northern margin of the BCB belongs to the European plate and exhibits a main NW-SE structural orientation (Fig. 2). This margin is adjacent to the Landes Palaeozoic massif (European plate) by the NE and is limited to the SW by the Leizta-Elgoibar fault which is assigned to the plate boundary between the Iberia and Eurasia plates (Agirrezabala, 1996; García-Mondéjar et al., 1996; and references therein). The stratigraphic architecture and sedimentologic characteristics of the Albian sedimentary record of the margin indicate an overall southwest sedimentary polarity (Agirrezabala, 1996). During the Albian the northern margin was sited at a palaeolatitude of ca. 35° with a subtropical warm and wet climate (Dercourt et al., 2000). Open sea waters on the margin were warm and with a normal salinity (García-Mondéjar, 1990).

In the last thirty years, the collection of an important sample of Middle and Upper Albian ammonoids hosted in offshore marine successions made possible the accurate dating of these successions. This collection is today hosted in the Department of Stratigraphy and Palaeontology of the University of the Basque Country (UPV/EHU; Leioa), in the Museo de Ciencias Naturales de Araba (MCNA; Vitoria-Gasteiz) and in the Nautilus Museum of the Basque Coast Geopark (NM; Mutriku, Gipuzkoa). However, no Lower Albian ammonoids have been

found up to date; the dating of this part of the succession has been possible by means of orbitolinids (foraminifers). The first references to ammonoids in the study area come from Gómez de Llarena (1958), Rat (1959) but they only refer to identifications of scarce specimens with biostratigraphic value. The only descriptive works on ammonoids of the study area are those of Wiedmann and Boess (1984) and Agirrezabala et al. (1992). Afterwards, the accurate biostratigraphy for the Middle-Upper Albian with indication of the associated species has been given in Agirrezabala (1996) and Agirrezabala et al. (2002) for the eastern part of the study area, and in López-Horgue et al. (2009) and López-Horgue and Bodego (2012) for the western part.

3. Methods

This paper presents a synthesis of stratigraphic, sedimentological and palaeontological data from twelve main Albian sections distributed along the northern margin of the BCB, summarized in a cross-margin transect to illustrate the history of the Albian environmental changes and local bioevents. In each section, detailed description and interpretation of sedimentary facies and collecting and study of fossils (principally ammonoid) have been carried out. A total of > 250 ammonoid specimens have been considered, spanning from the basal Middle Albian to the Upper Albian. These ammonoids were published in two previous papers by Agirrezabala et al. (2002) and López-Horgue et al. (2009). The correlation among the sections is based on ammonoid biostratigraphic data and, to a lesser extent, on inoceramid and foraminifera data. In addition, published detailed mapping of lithostratigraphic units, physical event deposits (megabeds, bentonite beds, volcanic flows) and erosional/non-depositional features (unconformities), and chemostratigraphic intervals (^{13}C -depleted deposits) are used as complementary correlation tools (Robles et al., 1988; Agirrezabala, 1996, 2009; Agirrezabala and García-Mondéjar, 1989). Thus, a margin-scale robust chronostratigraphic framework was obtained in which 6 ammonoid zones and subzones are distinguished, previously recognized by Agirrezabala et al. (2002) and López-Horgue et al. (2009). Although the specimen richness of collected ammonoids is not enough for an exhaustive statistical analysis, it is high enough for inferring major changes in the ammonoid assemblages, which may be related to environmental perturbations.

The study and correlation of the ammonoid faunas from the northern margin of the BCB allows us: i) to discriminate stratigraphic intervals with different diversities (number of species) at a resolution level of ammonoid biozones (maximum resolution for margin-scale correlations); ii) to distinguish ammonoid associations with different features (morphology, ornamentation and size of the conch, and palaeogeographical affinity); and iii) to recognize local bioevents. In this paper, we use the term “local bioevent” as a short-term evolutionary, ecologic and biogeographic change recorded in the fossil biota of a limited area (100 mi) in response to rapid environmental changes (see Kauffman and Hart, 1996); these environmental changes (tectonics, climate, sea-level, volcanism, chemistry, etc.) may also cause correlative changes in the sedimentological record (Kauffman and Hart, 1996). Finally, we discuss the interrelationships between the ammonoid record and the environmental changes deduced from both the sedimentary facies and depositional architecture.

4. Results

4.1. Albian sedimentary record

The main stratigraphic and sedimentologic characteristics of the Albian sedimentary record of the northern margin are documented in Robles et al. (1988), Agirrezabala and García-Mondéjar (1989) and Agirrezabala (1996). In addition, many specific and detailed geological studies have been recently carried out in the area. Fig. 3 depicts a synthetic NE-SW stratigraphic cross-section for the Albian record of the

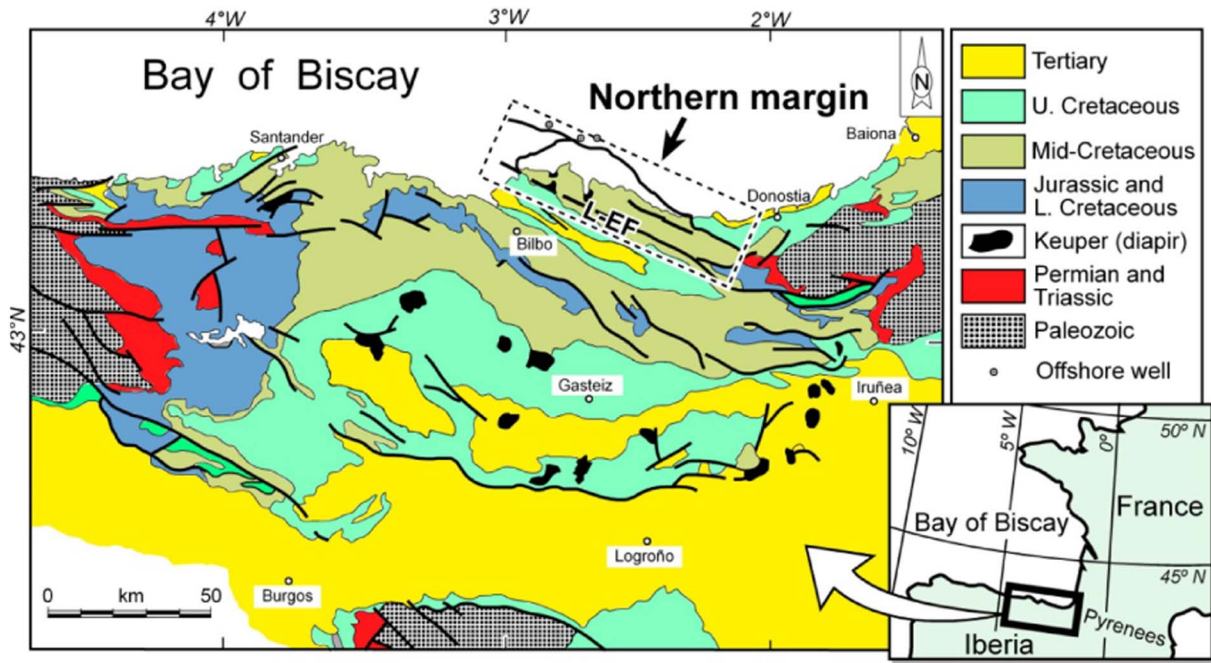


Fig. 2. Geologic map of the BCB with indication of the studied northern margin. L-E F: Leitz-Elgoibar fault.

northern margin where main sedimentary facies, stratigraphic sequences, and ammonoid biozones are shown. The Albian stratigraphic record can be divided into four main sequences bounded by the intervening unconformities U1 to U4. The sequence 1 is composed of deltaic to shallow-water marine deposits, and sequences 2–4 consist of deep-water clastic deposits (Black Flysch Group) and local shallow-water carbonates. The cross-section shows in a southwestward direction that: i) the Albian sedimentary record thickens greatly, ii) clastic deposits are progressively finer, and iii) sedimentary facies are pro-

gressively deeper water, indicating that during the Albian the margin had a southwestward sedimentary polarity with increasing subsidence in the same direction. It also shows NE- and N-trending transverse syndimentary faults that compartmented the margin during the Albian.

4.1.1. Sequence 1 (uppermost Aptian–Lower Albian)

The age of the bounding unconformity U1 and overlying basal deposits of this sequence is poorly constrained, ranging from uppermost

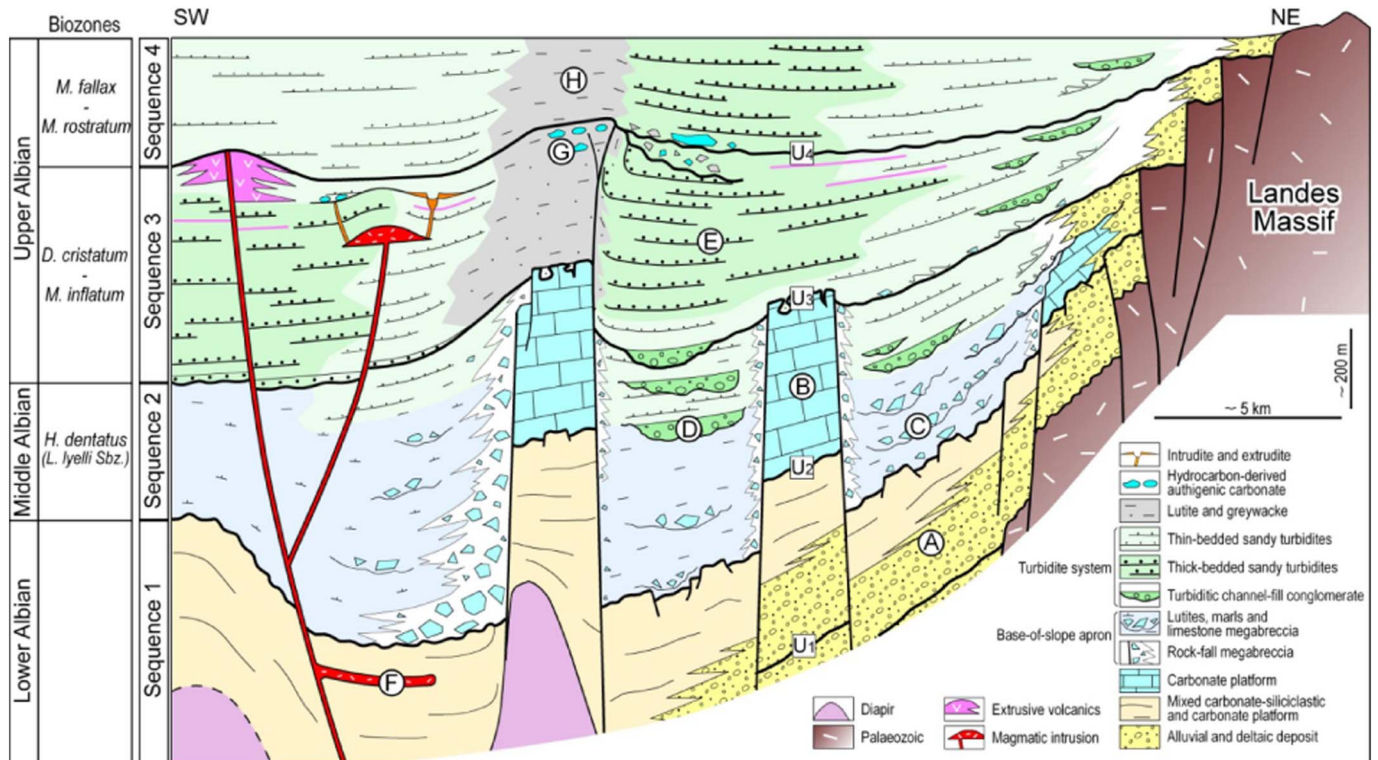


Fig. 3. Synthetic stratigraphic cross-section of the Albian northern margin deposits with indication of stratigraphic sequences (1–4), sequence boundaries (U2–U4) and main sedimentary facies. A–H letters indicate outcrop photographs shown in Fig. 4.

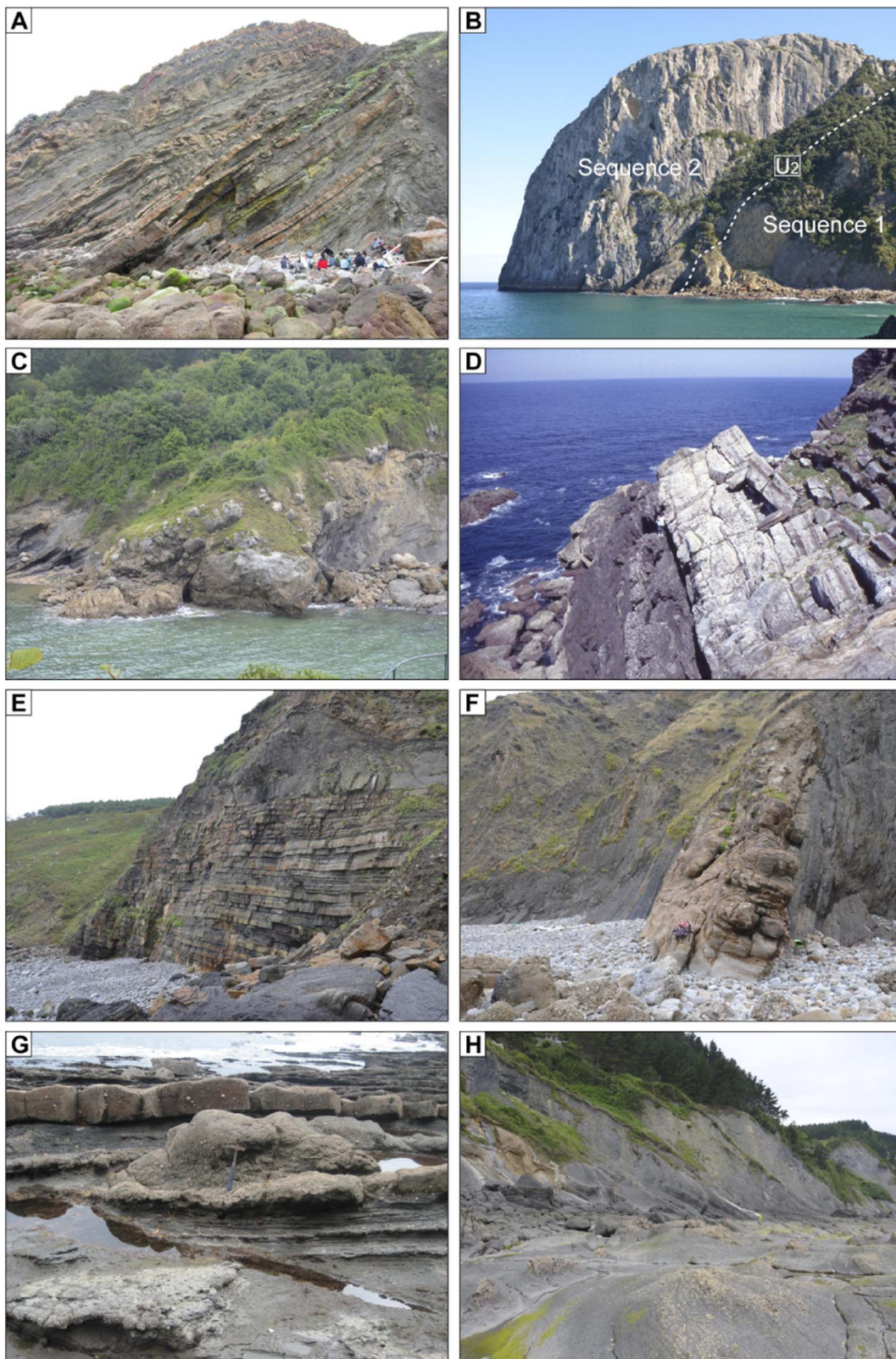


Fig. 4. Outcrop photographs of Albian tectono-stratigraphic sequences and main sedimentary facies (for location see Fig. 3). A) Deltaic sandstones and lutites arranged in thickening- and coarsening-upward sequences (sequence 1, Gorliz locality). B) Deltaic sandstone and lutites (sequence 1) overlaid by shallow-water massive limestones corresponding to a carbonate bank (sequence 2, Ogoño cape). C) Wedge-shaped limestone megabreccias with olistoliths up to 30 m long interbedded with organic-rich lutites (sequence 2, Ea locality). D) Turbiditic channel-fill composed of conglomerates and sandstones (sequence 2, Ea locality). Note a person for scale at the base of the channel-fill. E) Thick, parallel turbidite sandstones interpreted as turbidite lobe deposits (sequence 3, Bakio locality). F) 5 m-thick magmatic sill (sequence 3) intruded in organic-rich lutites (sequence 2). Contact aureole records formation of thermogenic methane, oil and CO₂ which migrated upward and escaped to the palaeoseabed (Gorliz locality). G) Hydrocarbon-derived authigenic carbonate lens filling a palaeopockmark (sequence 3, Ispaster locality). H) Mudstones deposited on a submarine structural palaeohigh under quiet, hemipelagic conditions (sequence 4, Mutriku locality).

Aptian to lowermost Albian. In the NE part of the margin, this sequence is composed of conglomerates, sandstones and organic-rich mudstones (Fig. 4A,B) interpreted as deposited in two retreating fan-delta systems (Robles et al., 1988; Agirrezabala, 1996) sourced from the NE. These deltaic systems pass southwestward to interbedded sandstones, mudstones and fossil-rich (rudists, corals, ostreids, orbitolinids, etc.) micritic and calcarenitic limestones deposited in a siliciclastic-carbonate mixed platform (Agirrezabala, 1996). More to the southwest, rudist- and coral wackestones dominate in a shallow-water carbonate platform. Marl deposits of slightly deeper intra-platform troughs occur locally and adjacent to carbonate platforms. This sequence was deposited in a general shallow-water marine environment with relatively gentle depositional gradients.

4.1.2. Sequence 2 (Middle Albian, *H. dentatus* Zone)

Basal bounding unconformity U2 is an erosive surface cross-cut by coeval NW- to NE-trending normal fault scarps. Some fault scarps show hardground features (borings, encrusting oysters and Fe mineral crusts), indicating their submarine exposition. Overlying deposits onlap fault scarps. The sequence is composed of two distinct deposit types: shallow-water limestones and adjacent deep-water resedimented clastic deposits. The boundaries between both deposit types are sharp and subvertical and are interpreted as syndepositional fault scarps. The shallow-water limestones are composed of massive rudistid and coral wackestones constituting lithosomes of reduce area (1–5 km²) but great thickness (up to 400 m) surrounded by deep-water deposits (Fig. 4B). They are interpreted as small aggrading carbonate banks formed on horsts or diapirs (Agirrezabala and García-Mondéjar, 1989; Poprawski et al., 2014).

The deep-water resedimented clastic deposits occur between the carbonate banks and fill NE-SW oriented fault-bounded grabens. They belong to the lowest part of the Black Flysch Group characterized by the presence of relatively organic-rich (TOC ca. 1%), black to dark gray lutites with abundant framboidal pyrite and *Zoophycos* ichnofacies; petrographic and Rock-Eval analyses indicate that organic matter was mainly of detrital character and derived from the continent (Agirrezabala et al., 2008, 2014). These deposits present two main parts, a lower calciclastic part and an upper siliciclastic part. The lower part is composed mainly of organic-rich lutites and thick limestone orto- and para-megabreccias with olistoliths up to 40 m long (Fig. 4C), with minor sandy turbidites. These deposits are interpreted as formed in a deep-water base-of-slope environment where quiet sedimentation (mud) was punctuated by down-slope catastrophic debris flow and rock falls (megabreccias) sourced from northern carbonate platforms. The upper part of the sequence is composed of coarse-grained siliciclastic turbidite systems characterized by proximal thick conglomeratic channel-fills (Fig. 4D) which pass down-slope to thinner tabular sandy turbidites interpreted as fan lobe and fan fringe deposits. These turbidite systems were sourced from northern fan-deltas and filled L-shaped pull-apart sub-basins (Agirrezabala and García-Mondéjar, 1994). In addition, limestone megabreccias with very limited lateral extension (200–400 m) and olistoliths with dimensions up to 280 × 40 m occur adjacent to carbonate banks, which are interpreted as rock fall deposits piled at the base of fault scarps (Agirrezabala and García-Mondéjar, 1988; Poprawski et al., 2014).

4.1.3. Sequence 3 (Upper Albian, *D. cristatum*–*M. inflatum* Zones)

Northern offshore wells document the presence of Upper Albian thin siliciclastic deposits overlying Palaeozoic rocks of the Landes Massif. Onshore, the lower boundary of the sequence (U3) is either a palaeokarst surface (top of the underlying carbonate banks) or an erosive surface. The existence of local angular unconformities and megabeds (seismites?) related to the lower boundary suggests a tectonic origin. The sequence boundary is overlaid by widespread deep-water siliciclastic deposits recording the drowning (after subaerial exposition) of the previous carbonate banks. The sequence consists of thick

turbidite systems filling fault-bounded subsident depocenters separated by structural highs. Turbidite systems are composed of tabular sandy turbidites showing *Nereites* ichnofacies, relatively organic-rich lutites (TOC ca. 1%) and siderite thin beds (Fig. 4E) interpreted as turbiditic lobe and fan fringe deposits. On structural palaeo-highs, bioturbated (*Zoophycos* ichnofacies) sandy lutites with scattered thin-bedded sandy turbidites and siderite beds are interpreted as the result of relatively quiet hemipelagic deposition punctuated by occasional diluted turbidity currents.

In addition, in the upper part of the sequence (*H. binum* Subzone–*M. inflatum* Zone), sedimentary deposits record different contemporaneous syn-depositional process, i.e. tectonic, magmatic, metamorphic and fluid expulsion processes. Local angular unconformities and related megabreccias record the transpressive deformation and uplift caused by sinistral vertical-axis block rotation of small cortical blocks in a strike-slip context (Agirrezabala et al., 2002; Agirrezabala and Dinarès-Turell, 2013). Basalts and pyroclastic deposits are interbedded with deep-water deposits (Agirrezabala and García-Mondéjar, 2001; Castañares et al., 2001), and magmatic laccoliths and sills intrude Albian sedimentary units (Fig. 4F). Intrusion of magmas caused syndepositional folding and fracturing of overburden rocks and formation of intrudites and extrudites (Agirrezabala et al., 2013; Agirrezabala, 2015). In the contact aureole of those magmatic intrusions, metamorphism of organic-rich host lutites led to the formation of overpressured hydrothermal fluids rich in thermogenic methane, oil and CO₂, which migrated upward and were expelled to the seabed (Agirrezabala et al., 2008, 2014). ¹³C-depleted authigenic carbonates occur in these seep areas (Fig. 4G) and enclose chemosymbiotic fauna, archea biomarkers, bitumen and non-obligate relatively rich fauna, i.e. abundant radiolarian and planktonic foraminifers, gastropods, bivalves, ammonoids, arthropods, sponges and rare corals (e.g. Agirrezabala, 2009, 2015; Agirrezabala et al., 2013). Some of these corals are zooxanthellate (Hannes Loeser, 2016, personal communication).

4.1.4. Sequence 4 (Upper Albian, *M. fallax* Zone)

In onshore outcrops, the basal bounding unconformity U4 shows different features basinwide: erosive surface, angular unconformity or onlap surface. The sequence is composed of thick- to thin-bedded tabular sandy turbidites showing *Nereites* ichnofacies interpreted as deposited in the distal part of submarine fans. These relatively thick turbidite deposits filled subsident depocenters separated by faulted ridges where hemipelagic mudstones were deposited (Fig. 4H). Locally, adjacent to these ridges, occurrence of angular unconformities and megabreccias record fault-related transpressive folding.

4.2. Albian ammonoid fauna

More than 250 specimens have been collected from the Albian succession of the northern margin of the BCB, spanning from the lower Middle Albian to the Upper Albian (see Fig. 2: sequences 2, 3 and 4); despite of the accurate field-exploration, Upper Aptian-Lower Albian sediments (sequence 1) did not yield ammonoids. In this sample, compiled in Table 1, a total of 58 species assigned to 34 genera and subgenera have been identified from all recognized biozones (Agirrezabala et al., 2002; López-Horgue et al., 2009). Ammonoids occur in 44 distinctive intervals of limited thickness, ranging between 5 and 6 cm and 4–5 m. Ammonoid occurrences are then widely distributed along the succession but are representative of the relative richness in these expanded series.

4.2.1. Ammonoid biostratigraphy

Ammonoid associations are representative of their corresponding biozones (Table 1). Biostratigraphy is well discussed and ammonoid associations represented in the works of Agirrezabala et al. (2002) and López-Horgue et al. (2009), where they follow the Albian zonal scheme for the Tethyan province proposed in López-Horgue et al. (1999) and

Table 1

Albian ammonite zones, subzones and ammonite content in the northern margin of the BCB. Data are compiled from Agirrezabala et al. (2002, 2003) and López-Horgue et al. (2009). We introduce here some modifications concerning the former Upper Albian *Stoliczkaia dispar* Zone, previously discussed in Gale et al. (2011) and Reboulet et al. (2014).

Zones, subzones and levels ^a	Ammonites
<i>M. fallax</i> – <i>M. rostratum</i> Zones. Levels: P, R, meters 551–563	
<i>Anisoceras</i> cf. <i>perarmatum</i> (Pictet & Campiche)	<i>Mortoniceras</i> (<i>Mortoniceras</i>) cf. <i>pachys</i> (Seeley)
<i>Anisoceras picteti</i> Spath	<i>Mortoniceras</i> (<i>Mortoniceras</i>) sp.
<i>Anisoceras pseudoelegans</i> (Pictet & Campiche)	<i>Anisoceras saussureanum</i> (Pictet)
<i>Mortoniceras</i> (<i>Mortoniceras</i>) <i>alstonense</i> (Breistroffer)	<i>Anisoceras armatum</i> (J. Sowerby)
<i>Mortoniceras</i> (<i>Mortoniceras</i>) <i>arietiforme</i> group Spath	<i>Mortoniceras</i> (<i>Mortoniceras</i>) sp. indet. cf. gr. <i>rostratum</i>
<i>Mortoniceras</i> (<i>Mortoniceras</i>) <i>rugosum</i> Spath	
<i>M. inflatum</i> Zone. Levels: N, meter 536	
<i>Hamitoides</i> cf. <i>studerianus</i> Pictet	<i>Lechites</i> sp.
<i>Cantabrigites</i> cf. <i>nanoides</i> Wiedmann	<i>Mortoniceras</i> (<i>M.</i>) <i>crassinodatum</i> (van Hoepen)
<i>H. varicosum</i> Zone (<i>H. hoffati</i> Subzone). Levels: K, L, meters 468–528	
<i>Puzosia</i> cf. <i>provincialis</i> (Parona & Bonarelli)	<i>Hypophylloceras velledae</i> (Michelin) ^d
<i>Hysterocheras</i> cf. <i>varicosum</i> (J. Sowerby)	<i>Idiohamites turgidus</i> (J. Sowerby) ^d
<i>Mortoniceras</i> (<i>Mortoniceras</i>) sp.	<i>Anisoceras arrogans</i> (Giebel) ^d
<i>Hamites</i> sp.	<i>Puzosia mayoriana</i> (d'Orbigny)
<i>Craginites</i> sp.	<i>Pachydesmoceras</i> cf. <i>denisonianum</i> ^d
<i>Mortoniceras</i> (<i>Deiradoceras</i>) <i>exilis</i> (van Hoepen) & cf. <i>ex.</i>	<i>Idiohamites</i> sp. ^c
<i>Arestoceras</i> cf. <i>splendidum</i> van Hoepen	<i>Mortoniceras</i> sp. ^c
<i>Mortoniceras</i> (<i>Deiradoceras</i>) <i>bispinosum</i> (Spath)	
<i>H. varicosum</i> Zone (<i>H. binum</i> Subzone). Levels: J, meters 455–475	
<i>Labeceras</i> sp.	<i>Desmoceras latidorsatum</i> (Michelin)
<i>Bhimaites</i> sp.	<i>Desmoceras</i> sp. juv.
<i>Hamites</i> sp. juv.	<i>Hypophylloceras moreti</i> (Mahmoud)
<i>Hysterocheras</i> sp. juv.	<i>Hypophylloceras subalpinum</i> (d'Orbigny)
<i>Kossmatella oosteri</i> Breistroffer	<i>Hypophylloceras seresitense</i> (Pervinquièrre)
<i>Hypophylloceras</i> sp.	cf. <i>Anagaudryceras</i> sp.
<i>Bhimaites</i> cf. <i>aontzyensis</i> Collignon	<i>Kossmatella schindewolfi</i> Wiedmann and Dieni
<i>Puzosia</i> (<i>Anapuzosia</i>) sp. juv.	<i>Kossmatella muhlenbecki</i> (Fallot)
<i>Kossmatella romana</i> Wiedmann	<i>Parasilesites kilianiformis</i> (Fallot)
<i>Tetragonites</i> sp. juv.	<i>Hysterocheras varicosum</i> (J. de C. Sowerby)
<i>Jauberticeras jaubertianum</i> (d'Orbigny) & cf. <i>jaubert.</i>	<i>Hysterocheras binum</i> (J. Sowerby)
<i>Protetragonites</i> sp. juv.	
<i>Puzosia mayoriana</i> (d'Orbigny)	<i>Puzosia</i> (<i>Anapuzosia</i>) <i>tucuyensis</i> (von Buch) and cf. <i>tuc.</i>
<i>D. cristatum</i> Zone– <i>H. varicosum</i> Zone (<i>H. orbigny</i> Subzone). Levels: G, I	
<i>Puzosia</i> sp.	<i>Oxytropidoceras</i> (<i>Oxytropidoceras</i>) cf. <i>cantianum</i> Spath
<i>Kossmatella</i> cf. <i>schindewolfi</i> Wiedmann & Dieni	<i>Kossmatella</i> ^b
<i>Hemiptychoceras</i> sp.	<i>Dipoloceras</i> ? ^b
<i>Puzosia</i> (<i>Puzosia</i>) sp.	<i>Ephiplites</i> ? ^b
<i>Hysterocheras</i> sp.	
<i>H. dentatus</i> Zone (<i>L. lyelli</i> Subzone). Levels: A, B, C, D, E, F, meter 430	
<i>Metahamites</i> cf. <i>elegans</i> (d'Orbigny)	<i>Lyelliceras pseudolyelli</i> (Parona & Bonarelli)
<i>Kossmatella</i> cf. <i>muhlenbecki</i> (Fallot)	<i>Lyelliceras</i> cf. <i>lyelli</i> (d'Orbigny)
<i>Metahamites</i> sp.	<i>Lyelliceras</i> cf. <i>gevreyi</i> (Jacob)
<i>Parasilesites</i> cf. <i>kilianiformis</i> (Fallot)	<i>Lyelliceras</i> sp. <i>peruvianum</i> -group
<i>Kossmatella</i> sp.	<i>Cleoniceras</i> (<i>Cleoniceras</i>) cf. <i>devisensis</i> Spath
<i>Eogaudryceras</i> sp.	<i>Protanisoceras</i> (<i>Protanisoceras</i>) sp.
<i>Dipolocerooides</i> sp.	<i>Puzosia</i> sp.
<i>Hemiptychoceras gaultinum</i> (Pictet)	<i>Oxytropidoceras</i> (<i>Oxytropidoceras</i>) sp.

Table 1 (continued)

Zones, subzones and levels ^a	Ammonites
<i>Kossmatella agassizianum</i> (Pictet)	<i>Oxytropidoceras</i> cf. <i>roissyanum</i> (d'Orbigny)

^a Letters A–R indicate levels of Agirrezabala et al. (2002, 2003; Table A1 and Fig. A1) and meters indicate levels of López-Horgue et al. (2009; Fig. 5).

^b Ammonites after Rat (1959).

^c Ammonites after Reitner (1987)

^d Ammonites after Pletsch (1990).

Owen (1999) with discussions in Wiedmann and Owen (2001) and Owen and Mutterlose (2006).

The Middle Albian is only represented by its basal biozone, the *Lyelliceras lyelli* Subzone of the *Hoplites dentatus* Zone, with 7 stratigraphic levels distributed in a sedimentary succession 100 to 500 m thick (sequence 2 in Fig. 3). Typical elements of this association, with 15 species from 11 genera/subgenera, are the marker *Lyelliceras lyelli* and *Oxytropidoceras* cf. *roissyanum*. A basin-wide unconformity separates Middle Albian sediments from the overlying Upper Albian succession (sequences 3 and 4 in Fig. 3).

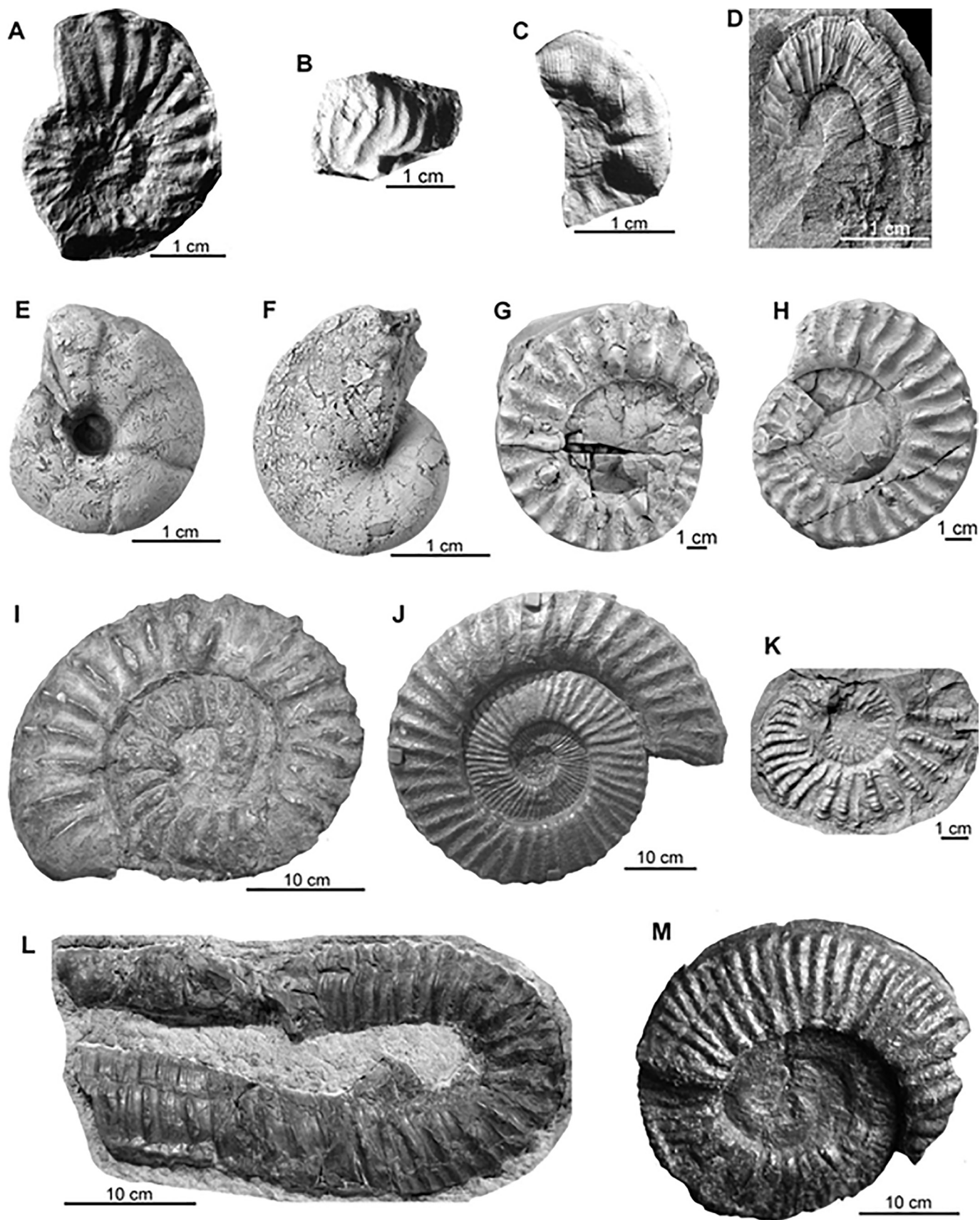
The Upper Albian sequence 3 in the study area is represented by the *Dipoloceras cristatum*, *Hysterocheras varicosum* and *Mortoniceras inflatum* Zones. Basal sediments of this sequence yield 2 levels with 7 species from 7 genera/subgenera corresponding to the *Dipoloceras cristatum* Zone and to the *Hysterocheras orbigny* Subzone of the *H. varicosum* Zone, with characteristic *Dipoloceras* sp. and *Hysterocheras* sp. Overlying *Hysterocheras binum* Subzone of the *H. varicosum* Zone is well represented by 6 levels; the marker *H. binum* occurs among 20 species distributed in 14 genera/subgenera. *Hysterocheras hoffati* Subzone of the *H. varicosum* Zone has been distinguished from an interval bearing 8 levels with a total of 13 species from 11 genera; typical elements of this Subzone are *Mortoniceras* spp. with a tendency to show a subtle mid-flank tubercle. *Mortoniceras inflatum* Zone sediments are characterized by an interval with 5 levels bearing *Mortoniceras* spp. with a mid-flank tubercle from a total of 4 species distributed into 4 genera/subgenera.

The Upper Albian sequence 4 is represented by the *Mortoniceras fallax* Zone and part of the *Mortoniceras rostratum* Zone, so not reaching the uppermost Albian. Corresponding sediments crop out in the Kardala and Armintza sea-cliffs, showing 16 levels with at least 10 species from 2 genera/subgenera; this association is characterized by *Mortoniceras* spp. transitional to typical *M. rostratum*. Ammonoids of the *M. inflatum*, *M. fallax* and *M. rostratum* biozones are currently being studied in more detail and will constitute the basis of a new paper.

4.2.2. Ammonoid-bearing levels and preservation

Ammonoids occur mainly in thin intervals of fine-grained siliciclastic sediments and associated diagenetic carbonates, being very scarce in coarse-grained sediments. Most of these levels originated in offshore marine areas adjacent to main terrigenous-dispersal systems, being rich in terrestrial organic matter.

Ammonoids from the lutites and calcareous muddy siltstones are preserved as crushed internal moulds with dissolved conch or replaced by diagenetic calcite, a finely preserved sculpture, entire body chambers and no signs of epibiont encrustation or boring (e.g. Fig. 5 A–D, K); in some intervals, the phragmocone is preserved as undistorted pyritic nucleus (e.g. Fig. 5 E, F). Ammonoids hosted in local hydrocarbon seep carbonates are common (Agirrezabala, 2009); hosted fossils usually preserve their original dimension (phragmocone and body chamber) but a shell replaced by diagenetic calcite. Siderite concretions are widespread in some fine-grained intervals and atop of some diluted turbidites; they bear well preserved undistorted ammonoids, with the conch (phragmocone and body chamber) preserved as diagenetic calcite, occasionally with its upper part dissolved, and no signs of epibionts (e.g. Fig. 5 G–J, L, M). In this type of concretions, delicate structures such as apertural rostra of *Mortoniceras* spp. are preserved.



(caption on next page)

Fig. 5. Ammonoids from the study area: examples of morphotypes and biogeographical/biostratigraphical references. A. *Lyelliceras* cf. *lyelli* (d'Orbigny) (UPV/EHU). B. *Cleoniceras* (C.) cf. *devisensis* Spath (UPV/EHU). C. *Kossmatella* cf. *schindewolfi* Wiedmann and Dieni (UPV/EHU). D. *Labeceras* sp. (MCNA 13472). E. *Desmoceras latidorsatum* (Michelin) (MCNA 13487). F. *Hypophylloceras subalpinum* (d'Orbigny) (MCNA 13502). G. *Mortonicer* (*Deiradoceras*) *exilis* (van Hoepen) (MCNA 13513). H. *Mortonicer* (*Deiradoceras*) *bispinosum* (Spath) (MCNA 13520). I. *Mortonicer* (*M.*) *rugosum* Spath (NM). J. *Mortonicer* (*M.*) *arietiforme* Spath (NM). K. *Craginites* sp. (UPV/EHU). L. *Anisoceras* sp. (NM). M. *Mortonicer* (*M.*) cf. *pachys* (Seeley) (NM). Specimens deposited in the collections of: UPV/EHU, the University of the Basque Country, department of Stratigraphy and Palaeontology, Leioa, Basque Country; MCNA, Museo de Ciencias Naturales de Álava, Gasteiz, Basque Country; NM, Nautilus Museum, Mutriku, Gipuzkoa, Basque Country.

Biozones		Morphotypes (%)	Examples
<i>M. rostratum</i>		1- Planorbicone to serpenticone (35) 2- Platycone to serpenticone (30) 3- Ancylocone (25) 4- Discocone (10)	1- <i>Puzosia</i> 2- <i>Mortonicer</i> 3- <i>Anisoceras</i> 4- <i>Hypophylloceras</i>
<i>M. fallax</i>			
<i>M. inflatum</i>		1- Spherocone to planorbicone-like (>35) 2- Planorbicone to serpenticone (35) 3- Platycone to serpenticone (<10) 4- Ancylocone (<10) 5- Orthocone (<10)	1- <i>Desmoceras</i> 2- <i>Puzosia</i> 3- <i>Mortonicer</i> 4- <i>Hamitoides</i> 5- <i>Lechites</i>
H. varicosum	<i>H. choffati</i>	1- Platycone to serpenticone (45) 2- Planorbicone to serpenticone (20) 3- Ancylocone (20) 4- Discocone (5) 5- Hamiticone (5) 6- Spherocone to planorbicone-like (5)	1- <i>Deiradoceras</i> 2- <i>Puzosia</i> 3- <i>Idiohamites</i> 4- <i>Hypophylloceras</i> 5- <i>Hamites</i> 6- <i>Pachydesmoceras</i>
	<i>H. binum</i>	1- Spherocone to planorbicone-like (>25) 2- Planorbicone to serpenticone (>25) 3- Discocone (20) 4- Platycone to serpenticone (15) 5- Ancylocones (<10)	1- <i>Desmoceras</i> , <i>Tetragonites</i> 2- <i>Puzosia</i> , <i>Kossmatella</i> 3- <i>Hypophylloceras</i> 4- <i>Parasilesites</i> , <i>Hysteroce</i> 5- <i>Labeceras</i>
	<i>H. orbigny</i>	1- Planorbicone to serpenticone (>70) 2- Platycone (<10) 3- Platycone to serpenticone (<10) 4- Hamiticone (<10)	1- <i>Puzosia</i> , <i>Kossmatella</i> 2- <i>Oxytropidoceras</i> 3- <i>Hysteroce</i> 4- <i>Hemiptychoceras</i>
<i>D. cristatum</i>		1- Platycone to serpenticone (40) 2- Planorbicone to serpenticone (35) 3- Platycone (15) 4- Hamiticone and Ancylocone (10)	1- <i>Parasilesites</i> , <i>Lyelliceras</i> 2- <i>Puzosia</i> , <i>Kossmatella</i> , <i>Dipoloceroi</i> 3- <i>Oxytropidoceras</i> 4- <i>Hemiptychoceras</i> , <i>Protanisoceras</i>
<i>H. dentatus</i>			

Key of morphotypes:

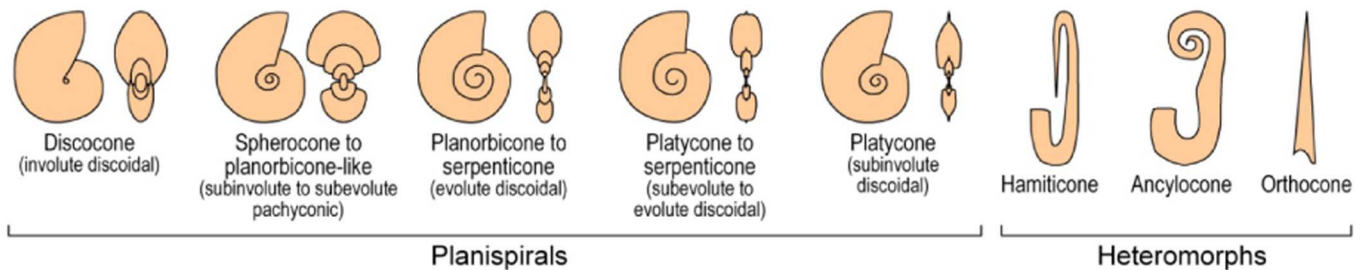


Fig. 6. Ammonoid morphotypes distinguished among studied associations with indication of the relative proportion in a given assemblage and representative examples. Based on the proportion of different morphotypes, associations are distinguished according to their zonal distribution. Morphotypes are illustrated in the lower part of the figure. Morphotypes after Westermann (1996) and Ritterbush and Bottjer (2012), with precisions on the planispiral shape sensu Korn (2010).

Fragments of ammonoids are rarely found in sandy turbidites, usually preserved as internal moulds.

4.2.3. Ammonoid morphology and size

We focus here on the description of the main ammonoids morphologies present in the studied area, their occurrence and variability through time. We follow the terminology of Westermann (1996) with the updates given by Ritterbush and Bottjer (2012) and compare them to the conch terminology of Korn (2010). Accordingly, we present here

eight morphological groups or morphotypes, each of them comprising related forms of different taxa, which are representative of life modes in the marine environment. In the Fig. 6 we summarize the distinguished morphotypes and their relative proportion in a given sample according to their zonal scheme. Despite the ammonoid sample is quite good with about 250 specimens distributed in 44 levels, the aim of this work is not to make an accurate analysis of the conch parameters and indeed the morphological variation, but to make a first attempt to present the main ammonoid morphotypes and their occurrences in a stratigraphic and

sedimentological frame.

Ammonite sizes range in diameter from several mm to almost 500 mm, being common up to 100 mm size. Biggest forms occur mainly in the *M. inflatum* to *M. rostratum* Zones interval where they are common. According to the size groups defined by Stevens (1988), these ammonites are of the “large” size-class; however, they really represent oversized (giant) forms if considering the median sizes of their family-level representatives. Concerning the conch ornamentation, we only differentiate planispiral leiostracan elements (such as the genera *Hypophylloceras*, *Desmoceras* and *Tetragonites*), planispiral trachyostracan elements (such as the genera *Lyelliceras*, *Mortoniceras* and *Cantabrigites*), and finely ribbed/strongly ribbed heteromorphs (e.g. *Labeceras*/*Anisoceras*) as a first attempt to differentiate conch sculptures from smooth to finely ribbed and strongly ribbed/tuberculated. In the BCB, we observe that less ornamented forms are common in offshore deeper environments, meanwhile ornamented forms are comparatively more abundant in offshore shallower areas (e.g. López-Horgue et al., 1999, 2009).

4.2.4. Ammonoid bioevents

Bioevents are levels or thin stratigraphic intervals with a distinctive fossil association characterized by exotic elements, striking abundance of a taxon and/or morphological changes (e.g. Wilmsen, 2008); they respond to short-term (up to ~100 kyr) evolutionary, ecologic and/or biogeographic turnovers of organisms due to changing environmental conditions, occurring at local, regional or global scale (Kaufman and Hart, 1996). The relative abundance of the ammonoids in the expanded sediment successions of the northern margin of the BCB, the accuracy of the stratigraphic studies (e.g. Agirrezabala et al., 2002) and the known biogeographical affinities of the ammonoids (López-Horgue et al., 1999, 2009) allow us to distinguish bioevents of the following types: a- evolutive changes, with first and last occurrences at generic level; b- palaeobiogeographical changes, determined by the variations of taxa of different affinities; c- abundance and diversity changes; d- changes in the morphotype composition of the ammonoid associations and in the shell size. These bioevents are shown in Fig. 7 and are the following: 1- sudden basal Middle Albian occurrence of the first ammonoids in the area after the total absence during the Late Aptian and Early Albian; the association is diverse and of Tethyan affinities, but with scarce typical South American and European elements; 2- first occurrences of cosmopolitan *Hysterocheras* sp. and European *Epihoplites* sp. in the Upper Albian *D. cristatum* Zone to *H. orbigny* Subzone transition, after an interval without sedimentary record of most of the Middle Albian; 3- incursion of the South African *Labeceras* sp. (López-Horgue et al., 2009) during the *H. orbigny* to *H. binum* subzones transition-time; 4- Tethyan leiostracan elements dominate in a well diversified association of mainly juveniles of the *H. binum* Subzone; 5- incursion of the typical North American *Craginites* sp. during times of the basal *H. hoffati* Subzone (López-Horgue et al., 2009); trachyostracan ammonoids (cosmopolitan but essentially Tethyan Mortoniceratinae) dominate with some South African elements; 6- last occurrence of *Hysterocheras* sp.; 7- first occurrence of *Mortoniceras* sp. in the area at around the middle part of the *H. hoffati* Subzone; 8- first occurrences of the heteromorphs *Idiohamites* sp. and *Anisoceras* sp. at around the middle part of the *M. inflatum* Zone, together with giant leiostracan forms of Tethyan affinities; 9- abundance of cosmopolitan ammonoids at the upper part of the *M. inflatum* Zone; and 10- giant trachyostracan (cosmopolitan but essentially Tethyan Mortoniceratinae), leiostracan (typically Tethyan Desmoceratidae) and spiny heteromorphs (Anisoceratidae) occur at the base of the *M. fallax* Zone, being the most common forms up to basal *M. rostratum* Zone.

5. Discussion: Albian environmental changes and bioevents

In this chapter we will focus on the integration of mainly ammonoid-based palaeontological data with stratigraphic and sedimentolo-

gical data from the studied Albian sedimentary record. Fossil preservation and host rock characteristics make the ammonoid associations be considered autochthonous, with null or very low degree of lateral transport (e.g. Fernández-López, 1991). Ammonoids are not considered facies-dependent (e.g. Lukeneder, 2015). Their common occurrence in fine-grained facies in domains without important coarse-grained input, suggest they were inhabitants of offshore (oceanic) waters with an important siliciclastic suspension input. Conch morphology and ontogenetic stages are primary elements to understand interpretations on ammonoid habitat, which together with their palaeobiogeographical affinities and the information obtained from the facies analysis, allow us to make a conceptual model of the environment inhabited by them in the northern margin of the Basque-Cantabrian Basin.

5.1. Margin water depth, width and connectivity

The Albian sequences record an important pulsating deepening and widening of the margin, which coincides with back-faulting pulses occurred at the sequence boundaries (U2–U4). During the Early Albian (sequence 1) the development of deltaic to platform environments indicates coastal to neritic water depths with low bathymetric gradients. At the earliest Early Albian (sequence 2), an important transtensive tectonic pulse faulted the northern margin and created a horst and graben system where shallow-water conditions maintained only on small, isolated uplifted blocks adjacent to deep-sea troughs developed on grabens. The deepening of these syn-tectonic depositional systems suggests that back-faulting widened the margin northeastward. During the Late Albian, after an erosion/non-deposition phase (Middle Albian pro parte), the instauration of an extensive and more distal deep-water environment (sequences 3 and 4) indicates a new deepening and back-faulting pulse. It is also supported by the occurrence in offshore wells of Upper Albian deposits overlying the Landes Palaeozoic massif (NE part in Fig. 3), as well as on other Palaeozoic massifs around the BCB (e.g. Bodego et al., 2015). The proliferation of planktonic microfossils (foraminifers and radiolarian) suggests that the deepening and widening of the margin led to the link with the open ocean (Bay of Biscay). Biofacies data suggest that most of the margin sea floor was located at mesopelagic depths (Castañares et al., 2001; García-Mondéjar et al., 2004). In this deep-water realm, structural ridges constituted hemipelagic palaeohighs, in which the presence of rare zooxanthellate corals and rudist indicates photic conditions and epipelagic water depths (< 200 m).

The sequence 2 yields a diverse association in which sculptured ammonoids (both trachyostracan planispirals and heteromorphs) comprise < 50% of the sample with respect to leiostracan planispirals. This ratio indicates offshore waters (e.g. Westermann, 1996; Kawabe, 2003) compatible with the suggested epipelagic to upper mesopelagic depths after sedimentological data. Despite being a less rich association, ammonoids from the basal sequence 3 (*D. cristatum* and *H. orbigny* biozones) also suggest a similar offshore environment. The association of the *H. binum* Subzone (sequence 3) is dominated by planispiral leiostracan juveniles, usually pyritized; there are also some inoceramids *Actinoceramus*. These Upper Albian inoceramids occur in variable oxygenated conditions (Crampton and Gale, 2005); their occurrence in the study area in muddy intervals with very scarce bioturbation and pyritic ammonoids may suggest hypoxic bottoms and a likely expansion of the oxygen minimum zone, in contrast to other muddy intervals with more bioturbation and lack of inoceramids and pyritic ammonoids. This interpretation is compatible with relative deeper conditions that can also be suggested by the dominance of leiostracan planispirals. The upper part of the sequence 3 and sequence 4 yield ammonoid associations in which leiostracan represent about 2/3 of the sample. This reflects the persistence of the offshore conditions in the study area.

Sea-water masses of different origin can be mixed due to the opening of seaways after different mechanisms such as tectonics and relative sea-level rises. The admixtures of ammonoids of different

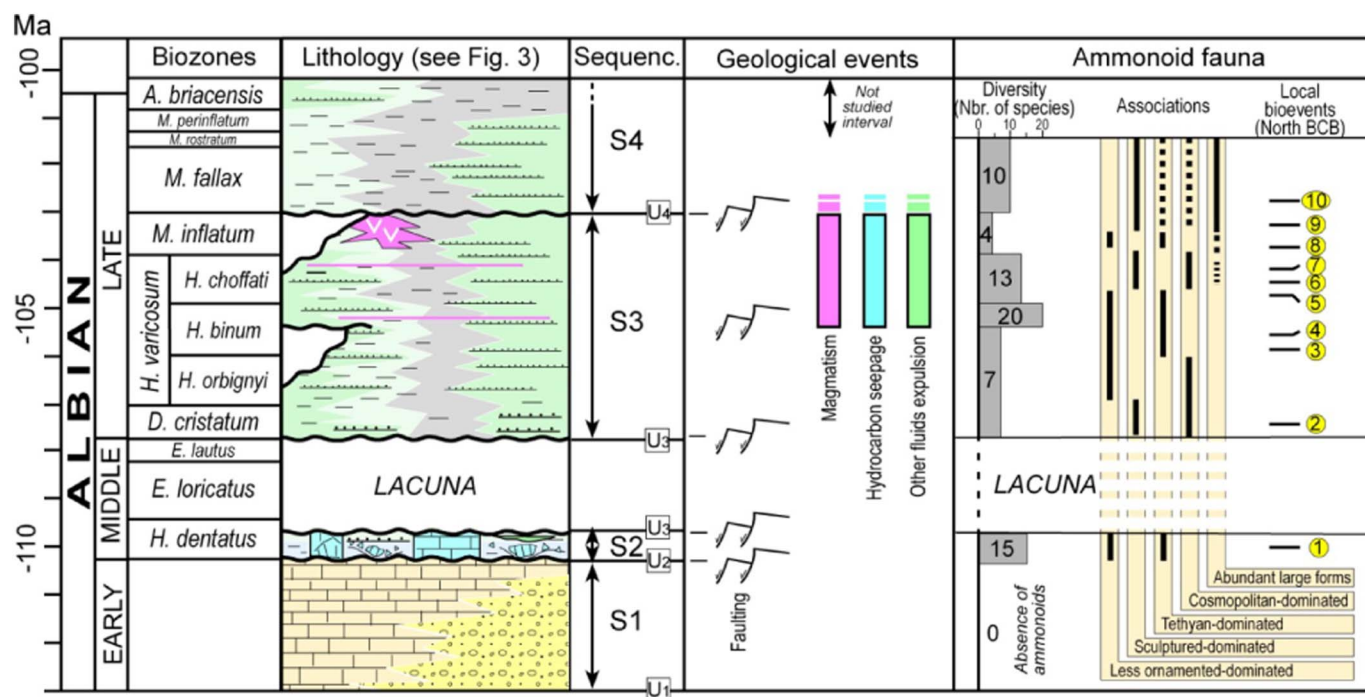


Fig. 7. Characteristics of ammonoid fauna from the northern margin of the BCB and time-correlation to the main geological events that controlled environmental conditions and basin development. Ammonoid biostratigraphy and other ammonoid occurrences as in López-Horgue et al., 2009. Other sources: Agirrezabala et al., 2013; Rat, 1959; Gómez de Larena, 1958; Reitner, 1987; Pletsch, 1990. U: Sequence-bounding unconformities. Circled numbers refer to main local bioevents and related steps of ammonoid turnover: 1- sudden occurrence of ammonoids (of the L. *Lyelli* Subzone) considered as the FO (first occurrence) for Albian ammonoids in the Northern margin of the Basque Cantabrian Basin; mainly a Tethyan association with cosmopolitan elements, western Tethys elements (*Lyelliceras* gr. *peruvianum*) and one specimen typical of the European province (*Cleoniceras* cf. *devisense*). 2- FO of *Hysterocheras* sp. and incursion of European *Epihoplites* sp. 3- Incursion of South African *Labeceras* sp. 4- Abundance of Tethyan elements and FO of *Desmoceras latidorsatum*. 5- Incursion of North American *Craginites* sp. 6- LO (last occurrence) of *Hysterocheras* sp. 7- FO of *Mortoniceras* sp. 8- FO of *Anisoceras* sp. and *Idiohamites* sp. 9- Abundance of cosmopolitan elements. 10- Onset of abundant cosmopolitan and Tethyan large elements.

biogeographical affinities or the punctuated introduction of species typical of other areas are evidences of sea connections (e.g. Lehmann et al., 2015). The studied area is dominated by Tethyan and cosmopolitan elements with punctuated incursions of exotic elements (as also indicated in the southern BCB; López-Horgue et al., 1999). Middle Albian is typically Tethyan but with elements from South America and Europe, indicative of a net connection of the basin after an important faulting phase. The margin preserved its connectivity for the entire Late Albian with punctuated incursions of ammonoids from other regions, mostly associated with tectonic pulses (Fig. 7): 1- north European elements during the early Late Albian; and 2- typical South African (e.g. Fig. 5 G) and North American (e.g. Fig. 5 K) elements, also coinciding with the onset of magmatism and seepage of hydrocarbons and other fluids in the margin.

5.2. Sea water column and sediment characteristics

The Early Albian shallow submarine environment (sequence 1) was subject to extensive reworking by waves and currents and was well oxygenated (García-Mondéjar, 1990). In Middle to Late Albian times (sequences 2–4) the deposition of deep-water black to dark gray lutites rich in organic matter, framboidal pyrite and siderite concretions indicate a muddy dysoxic sea floor (Potter et al., 2005). Here, aerobic oxidation of the organic matter caused depletion of oxygen in the shallowest sediments. At some greater burial depth (several centimetres) organic matter was oxidized in suboxic conditions by bacteria-mediated iron reduction, leading formation of early diagenetic pyrite and siderite (Gil et al., 1986). The quiet sedimentation of mud in the deep-sea was punctuated by gravity-driven flows of different concentrations, increasing temporary the energy, turbidity and oxygenation of the bottom waters.

Ammonoid morphotypes from the study area are indicative of a

demersal to planktic lifestyle in an offshore environment (e.g. Westermann, 1996; Ritterbush and Bottjer, 2012). The occurrence of demersal morphotypes (e.g. brancoceratids such as *Mortoniceras* sp.) is indicative of an oxygenated water column, since these forms do not survive in hypoxic conditions (e.g. Batt, 1993). Actually, these demersal forms are scarce or absent in the intervals with pyritized juveniles (e.g. *H. binum* Subzone), suggesting that oxygenated waters were only in the upper water column. Both planktic vertical migrants, such as *Hypophylloceras* sp. and *Jauberticeras* sp., and planktic drifters, such as *Desmoceras* sp., *Tetragonites* sp. and probably *Puzosia* sp., are abundant throughout the Upper Albian succession. Ammonoids are suggested to be of high metabolism (Lukeneder, 2015) and so they needed oxygenated waters. However, there are examples of associations of small heteromorphs in hypoxic facies (e.g. Lukeneder, 2007) which are interpreted to have been adapted to oxygen-deficient conditions for short time for preying or migrations; this scenario might be also suggested, although with cautions, for the abundant juveniles and small adults of the *H. binum* Subzone.

5.3. Magmatism, geofluids emissions and trophic level

During the early Late Albian (sequence 3, *H. binum* Subzone-*M. inflatum* Zone) magmatic activity led formation of high-level magmatic intrusions and submarine deposition of extrusive (effusive and explosive) rocks. Hydrothermal and submarine alteration of these magmatic rocks may have provided a larger-than-normal iron flux to the sea water. Many evidences link iron fertilization from volcanic eruptions to increases of primary productivity and fish abundance (Cather et al., 2009; Langmann et al., 2010). In the case of the northern margin of the BCB, the relatively abundance of altered magmatic rocks suggest that they may have constituted a significant iron source which could promote fertilization of the Albian sea waters.

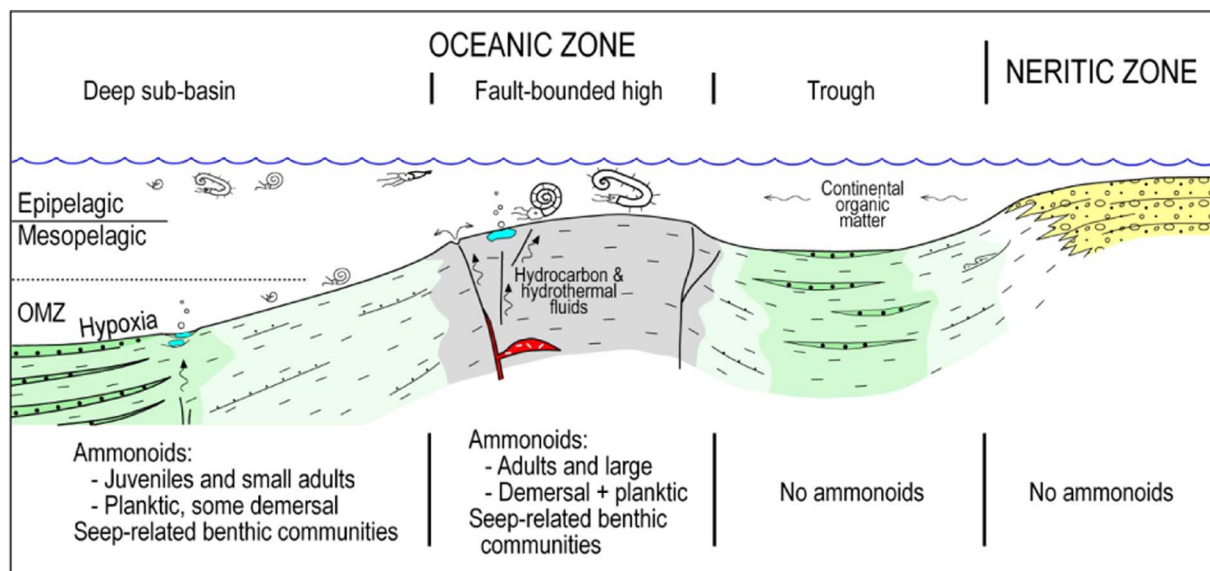


Fig. 8. Conceptual model of the different ammonoid habitats for the Late Albian of the northern margin of the BCB based on the integration of sedimentological and palaeontological data. Both groups of data suggest epipelagic to upper mesopelagic depths in an oceanic zone with distinct shallow areas on uplifted tectonic blocks surrounded by deeper sub-basins. Deeper areas were prone to develop hypoxia in the lower waters. Continent-derived organic matter and seepage of hydrocarbons and other hydrothermal fluids were the main nutrient sources. OMZ: oxygen minimum zone.

The formation of authigenic carbonates during the early Late Albian (sequence 3, *H. binum* Subzone-*M. inflatum* Zone) records the expulsion to the northern margin palaeoseabed of thermogenic methane, oil and CO₂ formed by contact metamorphism around magmatic intrusions (Agirrezabala et al., 2008, 2013, 2014; Agirrezabala, 2009, 2015). In these seeps, expelled hydrocarbons were anaerobically oxidized by microbial communities at or just below the seabed, promoting the precipitation of carbonate and constituting chemosynthetic oases in the largely deserted deep seabed (Agirrezabala, 2009; Agirrezabala et al., 2013). Here bacteria and archaea flourished and abundant chemosymbiotic megafauna inhabited the seabed, leading to an important biomass increment. This biomass may have constituted a food source which attracted non-obligate diverse megafauna species, finally contributing to an increase in the biomass. Moreover, seep carbonate formation at or near the seabed created local hardground substrates which could have been attractive to attached species, fishes and other megafauna (Judd and Hovland, 2007). The likely escape to the sea of hydrocarbons in the northern margin of the BCB could have also caused a fertilizing effect on the water column with an increase in the total nutrients and primary production, as invoked for present-day highly productive seas (Hovland et al., 2012; and references therein).

The relatively abundant organic matter of terrestrial origin throughout the studied succession suggests that the water-column was rich in continent-derived nutrients. Late Albian ammonoid associations changed due to variations in the primary production in the water column inferred from the study of calcareous nannofossils (SE France, Tethyan; Reboulet et al., 2005), recording changes from mesotrophic to oligotrophic conditions in the surface waters. *Anisoceras* sp. from offshore epipelagic habitats is suggested to be dominant, together with other heteromorphs, during mesotrophic conditions and more competitive than planispirals during oligotrophic conditions in surface waters; planispiral *Mortoniceras* sp. was suggested to inhabit the lower epipelagic zone with a demersal mode of life (Reboulet et al., 2005). Both morphotypes are common in the study area, being forms representative of planktic and demersal feeders in an area with fertilization in both deep and surficial waters.

5.4. Conceptual model on ammonoid habitats

Accordingly to the discussed environmental characteristics, ammo-

noids in the study area thrived in good conditions for most of the Late Albian: warm temperatures, enough nutrients, epipelagic to upper mesopelagic depths in oceanic waters (Fig. 8). Frequent incursions of other Tethyan elements and only one typical European specimen suggest no substantial changes in the water temperature. In this scenario, marine areas above shallower uplifted tectonic blocks in the study area show examples of large ammonoids. Temperature and nutrient availability may have triggered growth and maturity (Reboulet, 2001; Lukeneder, 2015). Size variations along a depth gradient, with larger forms in shallow waters, have been studied in the Early Cretaceous of South France (e.g. Reboulet, 1996); besides, dwarfed forms have been interpreted as size dependency on higher hydrostatic pressure (Reboulet, 2001). Isotopic studies in Cretaceous ammonoid conchs show an ontogenetic change of habitat, with early and adult stages inhabiting deeper and shallow areas respectively (e.g. Lukeneder et al., 2010), in accordance with previous studies suggesting a sexual and age separation in many ammonoid taxa (Kennedy and Cobban, 1976).

6. Conclusions

Albian ammonoids from the northern margin of the BCB provide a biostratigraphic framework for the sedimentary succession of the whole margin and allow us to distinguish 10 bioevents of three types: evolutionary changes, palaeobiogeographical changes, and abundance and diversity changes. The integration of ammonoid-based palaeontological data with stratigraphy and sedimentology data from the studied Albian sedimentary rocks indicates that bioevents are coeval to environmental and sedimentary changes. Time-correlation of faulting pulses with ammonoid bioevents indicates that Albian transtensive tectonics was ultimately the major control of the marine environmental changes. Transtensive tectonics triggered changes in the water depth, sea bottom physiography, seaways, sedimentary systems and sea-water chemistry. Accordingly, this two-fold study is the base for a conceptual model of the ammonoid habitats, in which adult and large forms dominated in fault-bounded epipelagic highs and juvenile and small ammonoids in deeper mesopelagic sub-basins.

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