

Ammonoid morphotypes from the upper Albian of the Basque-Cantabrian Basin: palaeoecology and relationship with the sedimentary facies

Morfotipos de ammonoideos del Albiense superior de la Cuenca Vasco-Cantábrica: paleoecología y relación con las facies sedimentarias

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ABSTRACT

In this work we present a morphological study of 65 planispiral ammonoid specimens occurring in the stratigraphic succession of the lower upper Albian of the central region of the Basque-Cantabrian Basin, northern Spain. The specimens correspond to the Zones of the ammonoids *Hysterocheras varicosum* and *Mortoniceras inflatum*. They are grouped into different morphotypes following the method of "Westerman Morphospace" which suggests diverse habitats for ammonoids, based on shell architecture and shape. The objective of this work is to check the likely correspondence of the suggested habitats with the information given by sedimentology. Accordingly, it has been possible to establish a distribution of the ammonoid ecomorphotypes demersal, nektonic, planktonic and vertical migrant, from shallow (neritic) to deeper marine areas (epipelagic to mesopelagic). The distribution of these ecomorphotypes with different bathymetric affinities is in agreement with the environmental interpretation of sedimentological data.

Key-words: ammonoid, upper Albian, morphotypes, palaeoecology, environment.

RESUMEN

Se han estudiado 65 especímenes de ammonoideos planoespirales de las Zonas de *Hysterocheras varicosum* y de *Mortoniceras inflatum* obtenidos de la serie estratigráfica correspondiente a la parte inferior del Albiense superior de la región central de la Cuenca Vasco-Cantábrica, norte de España. Los especímenes se han agrupado en diferentes morfotipos siguiendo su análisis mediante el método de "Westerman Morphospace", el cual sugiere diversos hábitats para ammonoideos, basado en la arquitectura y forma de la concha. El objetivo de este trabajo es contrastar la posible correspondencia de los hábitats con la información aportada por la sedimentología. De esta manera, se ha podido establecer una distribución de los ecomorfotipos de ammonoideos demersal, nektónico, planctónico y migrante vertical, en áreas marino someras (neríticas) a más profundas (epipelágicas a mesopelágicas). La distribución de estos ecomorfotipos con diferentes afinidades batimétricas se correlaciona de manera bastante precisa con la interpretación ambiental de los datos sedimentológicos.

Palabras clave: ammonoideo, Albiense superior, morfotipos, paleoecología, ambiente.

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Introduction

Ammonoid shell morphologies are frequently associated with different ways of life and habitats in the marine environment. The clustering in different morphotypes is associated with hypothetical habitats for planispiral ammonoids (Westermann, 1996), based on the architecture, shell function and relationship with sedimentary facies/biofacies (see also Batt, 1993). More recently, Ritterbush and Bottjer (2012) proposed the "Westermann Morphospace" method to

compare shell shapes of planispiral ammonoids based on the ideas of Westermann (1996) after quantification of the main shape parameters, namely umbilical ratio, thickness ratio and whorl expansion. Our aim is to check the use of the Westermann Morphospace method if compared to sedimentological data from the ammonoid bearing lithofacies. We have measured the shell shape parameters in order to hypothesize their relationships with sedimentary facies and changes in sea level as well as their importance as palaeoecological indicators.

Geological context

The study area is placed between the localities of Karrantza and Armintza (Biscay) and corresponds to a transect across the centre of the Basque-Cantabrian Basin for Albian times (Fig. 1A).

The lower Albian of Karrantza is characterized by shallow marine, rimmed carbonate platform systems with depositional slopes about 20° steep facing deeper marine siliciclastic troughs. Due to a huge input

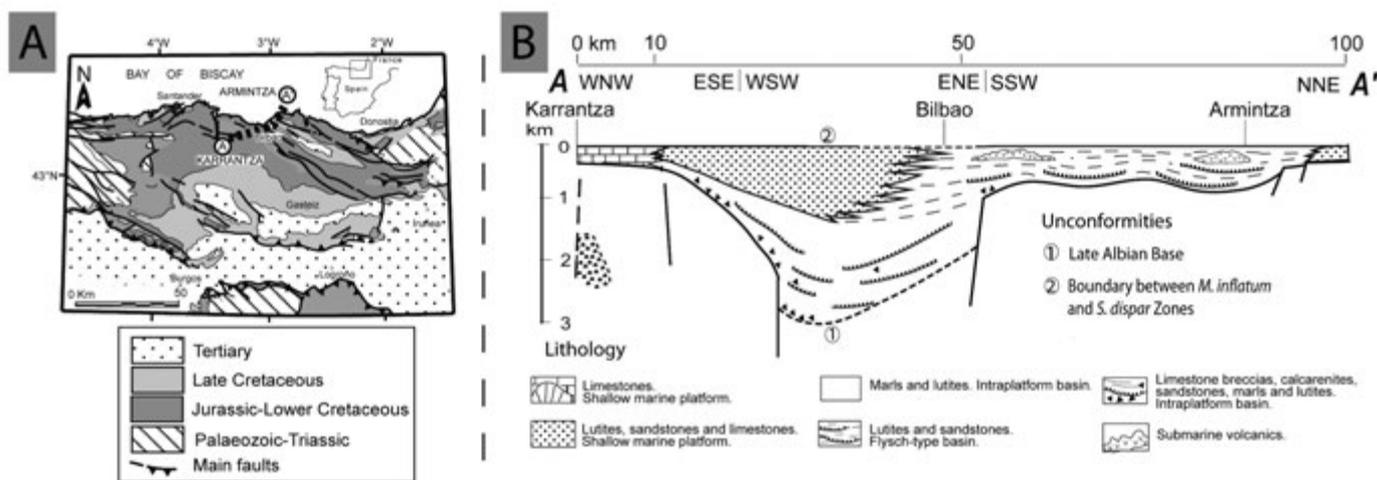


Fig. 1.- A) Outline of the geological map of the Basque-Cantabrian Basin and location of the cross-section shown in B. B) Stratigraphic cross-section to illustrate the relationship between the Karrantza and Armintza zones. Modified from López-Horgue *et al.* (2009).

Fig. 1.- A) Esquema del mapa geológico de la Cuenca Vasco-Cantábrica y la ubicación del corte estratigráfico de la figura B. B) Corte estratigráfico ilustrativo en el que se observa la relación entre las zonas de Karrantza y Armintza. Modificado de López-Horgue *et al.* (2009).

of siliciclastics during the upper Albian, carbonate platforms were buried or remained isolated in the more active structural highs (Fig. 1B) and deltaic to offshore siliclastic platforms and turbiditic troughs developed extensively. In this context, epipelagic and mesopelagic areas were recently proposed as ammonoid habitats according to shell shape and distribution and fossil-bearing facies (Agirrezabala and López-Horgue, 2017).

Deltaic sediments of the study area are grouped into the Valmeseda Fm. (García-Mondéjar, 1982) of late Albian age, but only ammonoids of the lower part of this formation are considered here (informal unit of La Escrita, of early late Albian age; López-Horgue *et al.*, 2009). This unit is time-equivalent to a remnant carbonate platform in the area (biostratigraphy based on ammonoids and orbitolinids; López-Horgue *et al.*, 2009). La Escrita unit is composed of shales and sandstones of coastal to shallow marine siliclastic origin, controlled by the action of tides and waves. Clay/silt-rich intervals would originate at moments of relative high sea level. On the other hand, sandy intervals have no equivalent in the carbonate platform and probably represent a filling of estuarine valleys during a relative low to rising sea level (López-Horgue *et al.*, 2009).

In the Armintza area, time-equivalent lutites and sandstones of turbiditic origin were deposited on deep troughs surrounded by tectonic highs with only clay/silt sedimentation. These deposits are interlayered with submarine basalts and volcanics.

Methodology

From a total of 130 planispiral ammonites published by López-Horgue *et al.* (2009), only 65 specimens (pertaining to 21 species) have been studied because of their good preservation in 3D, necessary for an accurate morphological study. Ammonites correspond to the upper Albian Zones of the ammonites *Hysterocheras variscosum* (Subzones of *Hysterocheras orbigny*, *Hysterocheras binum* and *Hysterocheras choffati*) and *Mortonicerat inflatum* (according to the biozonation proposed in López-Horgue *et al.*, 1999), from which 39 belong to the Karrantza area and the remaining 26 to the Armintza area. Most specimens are adults; the ontological stage is here indicated where necessary.

The method of Westermann Morphospace (Ritterbush and Bottjer, 2012) allows one to show the fundamental morphotypes and to hypothesize ammonoid lifestyles and habitats. The theoretical morphology of the shell of the ammonoids (Raup, 1966) is the basis to characterize mathematically the shape of the shell, with its main form being the logarithmic spiral (Raup, 1967). In the Westermann Morphospace method it is possible to quantify the morphotypes proposed by Westermann (1996) using the following parameters: U (umbilical diameter/diameter ratio), Th (shell width at a given diameter/diameter ratio) and W (whorl expansion rate; *i.e.*, maximum height/minimum height ratio at the maximum diameter). The results (for detailed procedure see Ritterbush and

Bottjer, 2012) are visualized in a ternary diagram, in which the vertices represent the basic ecomorphotypes and define the basic ecomorphospaces: serpenticonic (planktonic), spherocone (vertical migrant) and oxicone (nektonic). The central upper part of the diagram represents the demersal ecomorphospace. Considering the huge amount of calculations made in this work for 21 species, we only show here an example of the resulted diagrams corresponding to the *H. binum* Subzone with a rich representation of species (Fig. 2).

Resulted habitats from the morphological study are finally integrated with the overall sedimentological data and presented stratigraphically in order to check the correlation in both data groups and the method confidence.

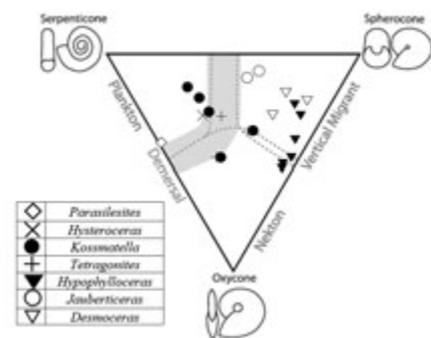


Fig. 2.- Ternary diagram in which ecomorphotypes have been established for the specimens belonging to *H. binum* Subzone in the study area (following Ritterbush and Bottjer, 2012).

Fig. 2.- Diagrama ternario en el que se han establecido los ecomorfotipos para los ejemplares pertenecientes a la Subzona de *H. binum* en la zona de estudio (acorde a Ritterbush y Bottjer, 2012).

Results

Results are presented according to ammonoid family levels within shallow to deeper marine environments indicating their biostratigraphical occurrence. We avoid indicating the species author in order to clarify the text (for this see López-Horgue *et al.*, 2009).

Family Phylloceratidae: *Hypophylloceras* specimens are all juveniles especially common in offshore facies. In Karrantza the genus occurs in *H. binum*-*H. choffati* Subzones, showing a nektonic affinity. In Armintza, *Hypophylloceras subalpinum*, *H. seresitense* and *Hypophylloceras* sp. occur in the *H. binum* Subzone, showing a nektonic to vertical migrant affinities.

Family Gaudryceratidae: in Karrantza, two pre-adults of *Kossmatella muhlenbecki* and *Kossmatella* sp. occur in the Subzones of *H. orbigny*, *H. binum* and *H. choffati*. Two adults of *Kossmatella romana* and *K. muhlenbecki*, occur in the subzone of *H. choffati*. All of these four specimens are of demersal affinity. In Armintza, in the *H. binum* subzone, we found 5 specimens of the species *Kossmatella oosteri*, *Kossmatella* sp., *K. schindewolfi* and two specimens of *K. romana*. Although most of them fall in or near the demersal ecomorphospace, *Kossmatella* sp. (juvenile) and *K. schindewolfi* (preadult) tend to a nektonic affinity, and *K. romana* (adult) and *K. oosteri* (juvenile) to a planktonic one.

Family Tetragonitidae: Juveniles of *Tetragonites* sp. have been found in the deeper marine facies of the *H. binum* Subzone together with juveniles of *Jauberticeras jaubertianum*. *Tetragonites* sp. shows a demersal affinity, meanwhile *J. jaubertianum* bears a vertical migrant tendency.

Family Desmocerotidae: the genus *Desmoceras* is only represented by *D. latidorsatum* occurring in shoreface to offshore facies. In Karrantza, 10 specimens of this species occur in the biozones of *H. binum*, *H. choffati* and *M. inflatum*; five specimens are juveniles from the *H. choffati* Subzone. They show a vertical migrant affinity, although there are also three demersal specimens. In Armintza, three specimens occur in the subzone of *H. binum*. They are juvenile vertical migrants. Therefore, most of *D. latidorsatum* are vertical migrants with only few examples of demersal affinity. From the genus *Puzosia*, *P. provincialis* occurs in Karrantza area, in shoreface facies of the *H. binum* and *H. choffati* Subzones. In Armintza, *P. mayoriana* occurs in deeper facies

of the *H. choffati* Subzone, in any case they all are adults of demersal affinity.

Family Brancoceratidae: The genus *Hysterocheras* is especially abundant in offshore facies of the shallow marine environments from Karrantza area. Here, adults of the species *H. carinatum* occur in the *H. orbigny* Subzone; *H. aff. varicosum* occurs in the *H. binum* Subzone; *H. choffati* and *H. bucklandi* occur in the *H. choffati* Subzone; and a juvenile *Hysterocheras* sp. occurs in the *M. inflatum* Zone. With a common demersal affinity, only some of them fall nearby planktonic (e.g., the *Hysterocheras* sp. juv.) and nektonic affinities. In the deeper marine facies of Armintza, an adult *H. binum* from the homonym Subzone is also of demersal affinity.

In Karrantza, the occurrence of the rest of *Brancoceratidae* in offshore facies is as follows: *Mortonicerias prerostratum* in the *H. binum* Subzone; *Mortonicerias* n. sp. and

Goodhallites balmatianum juv. in the *H. choffati* Subzone; and *Mortonicerias kiliani* in the *M. inflatum* Zone. All of them bear a demersal affinity but *M. prerostratum* shows a vertical migrant tendency.

In Armintza, *Mortonicerias* specimens occur in the *H. choffati* Subzone. All are adults, but *M. exilis* falls in the demersal ecomorphospace and the other two *M. bispinosum* in the planktonic one.

Discussion

Morphotypes and sedimentary facies

The lack of size selection and abrasion features in the fossils, and the occurrence of scarce broken shells only in tractive facies let us consider the ammonoids to be autochthonous and demic (following Fernández-López, 1991).

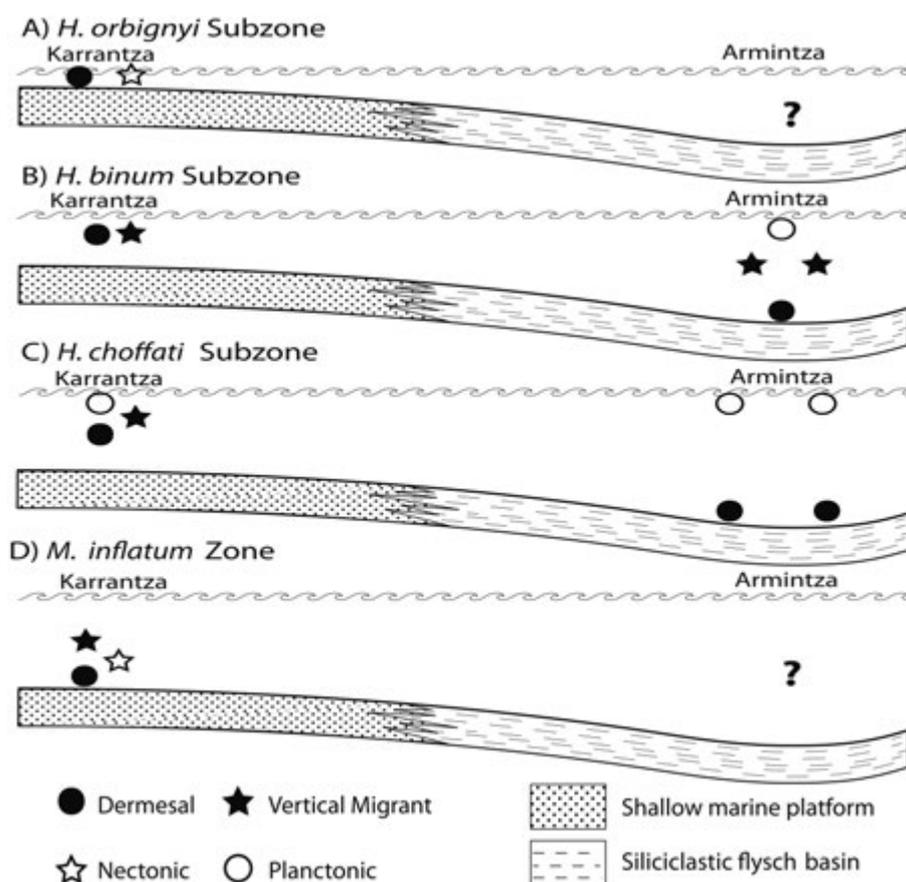


Fig. 3.- Interpretative bathymetric changes from *H. orbigny* to *M. inflatum* Biozones of Karrantza-Armintza. A) *H. orbigny* Subzone, shallow bathymetries. B) *H. binum* Subzone, vertical migrants indicate an increase of depth. C) *H. choffati* Subzone a planktonic specimen appear in Karrantza. D) *M. inflatum* Zone, increase of depth. Not to scale.

Fig. 3.- Cortes interpretativos de la evolución batimétrica desde la biozona de *H. orbigny* hasta la de *M. inflatum* de Karrantza-Armintza. A) Subzona de *H. orbigny*, paleobatimetrías someras. B) Subzona de *H. binum*, aparición de migrantes verticales implica un aumento de la profundidad. C) Subzona de *H. choffati*, aparece un ejemplar planctónico en Karrantza. D) Zona de *M. inflatum*, aumento de la profundidad. Sin escala.

In the shallow marine offshore facies of Karrantza area, demersal ammonoids are dominant (65%). *Desmoceras latidorsatum* is the only one with a vertical migrant affinity (15%). About 12% of the association of this area bears nektonic affinity. The remaining 8% shows planktonic affinity. The good preservation and the occurrence in micritic limestones and lutites atop of sandy parasequences in offshore facies (deepening after rapid flooding) suggest little or null transport. Suggested shallow platform bathymetry is in accordance with the abundance of demersal species.

In the sandy shoreface facies the occurrence of ammonoids is minimal, with two demersal specimens of the genus *Hystero-ceras* and *Knemiceras*. Same facies of the *H. binum* Subzone and *M. inflatum* Zone bear *Desmoceras latidorsatum* adult and juvenile both with vertical migrant affinity. Shoreface tractive sandstones may suggest a post-mortem transport of the ammonoids from shoreface-offshore transition areas.

In Armitza, most of the ammonoids are vertical migrants instead (42%); in the rest 31% are demersal, 20% planktonic and 7% nektonics. This fact suggests a deeper marine area than in nearshore-offshore areas of Karrantza due to the dominance of water-column habitat-preferences of the ammonoids. This agrees with the ammonoid-habitat model of Agirrezabala and López-Horgue (2017) for the northern margin of the Basque-Cantabrian Basin (where Armitza is located), in which ammonoids are considered to inhabit epipelagic and mesopelagic environments.

Changes in the sea level

After the given analysis it looks plausible to make an attempt to propose changes in palaeobathymetry (related to sea-level change) along time in the study area in connection with the habitat of the ammonoids (Fig. 3).

In the *H. orbigny* Subzone of the Karrantza shallow marine facies (Fig. 3A), de-

mersal and nektonic forms are in agreement with the common bathymetry of continental platforms. In the *H. binum* Subzone (Fig. 3B), the occurrence of a *Mortoniceras prostratum* with a vertical migrant affinity would indicate comparatively deeper waters and therefore a deepening of the area, with respect to the environment represented for the *H. orbigny* Subzone.

In the top of *H. binum* and in the *H. chofati* Subzones adult ammonoids are mainly demersal and some planktonic, while juveniles are nektonic and vertical migrants. This could indicate a subtle increase in paleobathymetry compared to the *H. binum* Subzone (Fig. 3C). Demersal and planktonic affinities of adult *Mortoniceras* spp. of the Armitza area are in agreement with ongoing deeper conditions in that zone.

In the *M. inflatum* Zone (Fig. 3D), relative abundances of nektonic and vertical migrant ammonoids (both 60%) may suggest again an increase in sea-depth. This is in concordance with an increase of tectonic subsidence for the *M. inflatum* chron with respect to the previous Subzone chrons, that ultimately caused increases of bathymetry (García-Mondéjar *et al.*, 2005).

Conclusions

The method of "Westermann Morphospace" is a good approach in order to understand the distribution of the ammonoid morphotypes and their ecological significance in sedimentary successions with good stratigraphic and sedimentological control. In this work the studied morphotypes and their ecological affinities correlate quite accurately with the sedimentological interpretations and stratigraphical analysis. The studied ecomorphotypes reflect different ways of ammonoid life from shallow (neritic, shelf) to deeper marine (epipelagic to mesopelagic) habitats.

The genus *Desmoceras*, showing a vertical migrant way of life in shoreface facies, is probably one of the found few cases of likely post-mortem drift.

A wider sample would be needed in order to detail the models both of habitats and of bathymetry changes for the different parts of the whole basin.

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