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Cephalopod assemblages and depositional sequences from the upper Cenomanian and lower Turonian of the Iberian Peninsula (Spain and Portugal)

Asociaciones de cefalópodos y secuencias deposicionales en el Cenomaniense superior y Turoniense inferior de la Península Ibérica (España y Portugal)

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Abstract

The comparison and correlation of the biostratigraphic successions identified in the upper Cenomanian and lower Turonian of the Iberian Trough (IT, Spain) and the Western Portuguese Carbonate Platform (WPCP, Portugal) allows differentiating nine cephalopod assemblages (1 to 9), with notably different taxa, and two (3rd order) depositional sequences (A and B). Some of these main intervals can be divided in minor ones, such as assemblage 4 (in 41 and 42) and sequence B (in B1 and B2). Assemblages 1 to 3 are related with sequence A, and assemblage 4 to 9 with sequence B (specifically, 4 to 6 with B1, and 7 to 9 with B2). The analysis and interpretation of these biostratigraphic data allows us to infer certain palaeoecologic turnovers that happened in the studied basins, both with external origin or due to local tectonic and palaeogeographical changes. Though partially altered by hypoxic phenomena (especially the sequence B1, assemblage 4) and local tectonics (mainly in the WPCP), in each of these cycles there were events of extinction of the cephalopods from shallow environments and survival of those from pelagic or deep environments, of settling of new environments, and of adaptation to them caused, successively, by intervals of low, ascending and high sea-level.

Keywords: Cephalopoda, fossil assemblage, depositional sequence, upper Cenomanian, lower Turonian, Iberian Peninsula

Resumen

La comparación y correlación de las sucesiones bioestratigráficas identificadas en el Cenomaniense superior y Turoniense inferior del Surco Ibérico (IT, España) y la Plataforma Carbonatada Occidental Portuguesa (WPCP, Portugal) permiten diferenciar nueve asociaciones de cefalópodos (1 a 9), con taxones notablemente diferentes, y dos secuencias deposicionales principales (3er orden) (A y B). Algunos de estos intervalos principales pueden dividirse en secundarios, como la Asociación 4 (en 41 and 42) y la Secuencia B (en B1 y B2). Las asociaciones 1 a 3 pueden se pueden relacionar con la secuencia A, y la asociación 4 a 9 con la secuencia la B (concretamente, 4 a 6 con B1, y 7 a 9 con B2). El análisis y la interpretación de estos datos bioestratigráficos permiten deducir ciertos cambios paleoecológicos sucedidos en las cuencas estudiadas, tanto de origen externo como debidos a la tectónica local ó a cambios paleogeográficos. Aunque parcialmente alterados por fenómenos de hipoxia (especialmente la secuencia B1, asociación 4) y de tectónica local (principalmente en el WPCP), en cada uno de estos ciclos se produjeron fenómenos de extinción de los cefalópodos de medios someros y de supervivencia de los de ambientes pelágicos ó profundos, de colonización de nuevos espacios, y de adaptación a los mismos provocados, sucesivamente, por intervalos de nivel de mar bajo, ascendente y alto.

Palabras clave: Cephalopoda, asociación fósil, secuencia deposicional, Cenomaniense superior, Turoniense inferior, Península Ibérica

1. Introduction

The well-marked relative sea-level changes during the late Cenomanian and early Turonian have been widely recorded in the Iberian Peninsula, especially when carbonate or mixed sequences are concerned. These facies yielded a diverse ensemble of boreal and meridional cephalopod assemblages, which allow the establishment of detailed stratigraphic settings and interregional correlations with Western Europe, North Africa and, even, the Western Interior of the USA.

Both the Spanish and Portuguese domains have a long historical tradition, from the early 19th century, of research on the stratigraphy and palaeontology of the Upper Cretaceous, and are especially known for their meridional ammonite assemblages with vascoceratids and associated temperate and warm faunas, mainly acanthoceratids and pseudotissotiids. Unfortunately, with only few exceptions, such as the Iberian Field Conference on Mid Cretaceous Events of 1979, these investigations have been carried out separately, without significant shared field-works, discussions or conclusions. With the purpose to join common efforts on this matter, next work presents a first concise synthesis and correlation of the Iberian cephalopod biostratigraphy for the upper Cenomanian and lower Turonian, considering the advances of the last decades on the Upper Cretaceous palaeontology and biostratigraphy.

Field work was carried out in outcrops with upper Cenomanian and lower Turonian sequences situated in the localities of Puentedey and Soncillo, in the north of the province of Burgos, of Fuentetoba and Villaciervos, in the centre of Soria, and of Cantalojas, Galve de Sorbe, Condemios, Somolinos, Atienza and Tamajón, in the north of Guadalajara, Spain. Within Portugal, the exposures of Salmanha-Figueira da Foz, Costa d'Arnes, Tentúgal, Ançã-Trouxemil, in the west of the province of Beira Litoral, and of Olival, Leiria and Nazaré, in the north of Estremadura, were sampled (Text-fig. 1). These Spanish sections are distributed along the southeastern Cantabrian Ranges, the southwestern Iberian Ranges and the northeastern Central System, whereas the Portuguese ones are located between the Atlantic Coast, the uplifted Jurassic Massifs of Estremadura, and the western border of the Hesperian Massif.

2. Historical background

Both the Iberian Trough and the Western Portuguese Carbonate Platform successions have been exhaustively studied since the late 19th century. During the 60's and 70's of the 20th century, when Wiedmann worked on the Spanish cephalopods, and Ferreira Soares and Berthou on the correlative palaeofaunas of Portugal, there has been a substantial advance in the knowledge about the ammonite assemblages. In the last decades, the ammonite palaeofaunas from the upper Cenomanian and lower Turonian of Western Portugal have been methodically reviewed by Callapez (1998) and Callapez and Ferreira Soares (2001), with recognition of new meridional ammonite assemblages with North African affinities. Identical work has been done by Barroso-Barcenilla (2006) in the Iberian Trough, but with the advantage of a larger field-work area with more expanded successions and deeper water facies. However, there has not been a tradition of comparing the Spanish and Portuguese faunal and stratigraphic settings, in order to set up an integrated biostratigraphic model with obvious implications on further palaeogeographic interpretations.

2.1. Iberian Trough

From the end of the 19th and the beginning of the 20th centuries many systematic and biostratigraphic studies on the cephalopods collected from the upper Cenomanian and lower Turonian of the Iberian Trough were carried out, but only a few of the studied specimens were described and illustrated in an appropriate way. Among

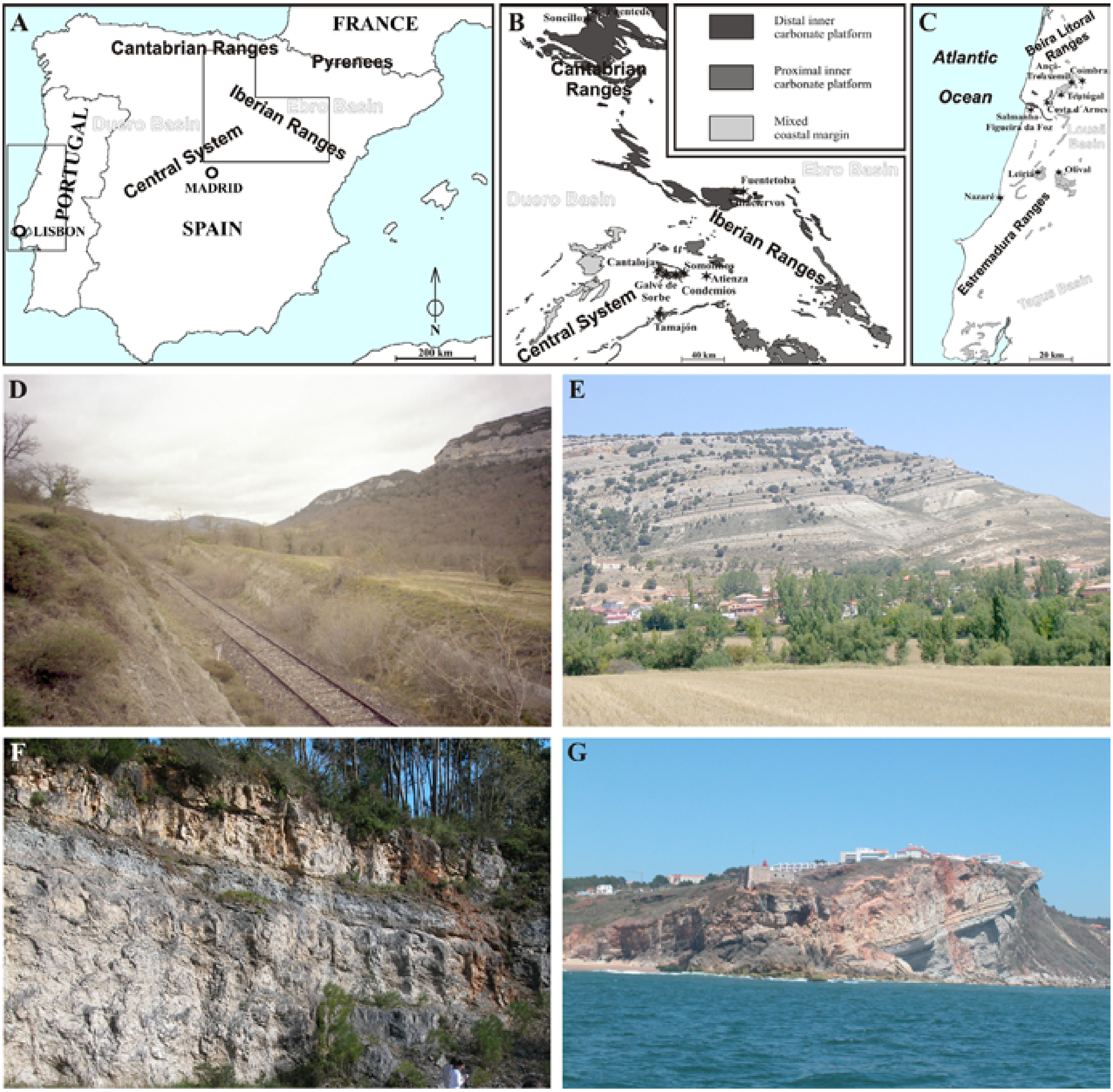


Fig. 1.- Geographic general location (A) and stratigraphic context of the main Spanish (B) and Portuguese (C) studied sections and other mentioned places. Photographic views of the outcrops of Puentedey (D), Condemios (E), Salmanha (F) and Nazaré (G).

Fig. 1.- Situación geográfica general (A) y contexto estratigráfico de las principales secciones españolas (B) y portuguesas (C) estudiadas y otros lugares citados. Vistas fotográficas de los afloramientos de Puentedey (D), Condemios (E), Salmanha (F) y Nazaré (G).

these works, those by Mallada (1891, 1892), Karrenberg (1935), Wiedmann (1960, 1964, 1975a, 1975b, 1979), Mojica and Wiedmann (1977), Wiedmann and Kauffman (1978), Segura and Wiedmann (1982), Carretero-Moreno (1982), Meléndez-Hevia (1984), Santamaría-Zabala (1991, 1992, 1995), Gräfe and Wiedmann (1993), Martínez *et al*. (1996), Küchler (1998), Barroso-Barcenilla (2004, 2006, 2007), Barroso-Barcenilla and Goy (2007, 2009, 2010) and Barroso-Barcenilla *et al*. (2009) stood out.

The sequence stratigraphy of the Upper Cretaceous of the Iberian Trough was studied in detail by several authors, such as Gräfe and Wiedmann (1993, 1998) and Gräfe (1994, 1996), in the Outer Navarro-Cantabrian Platform and the North-Castilian Sector; and Segura *et al*. (2001), Gil *et al*. (1993), Gil (1994), Gil and García (1996) and García-Hidalgo *et al*. (2003), in the Central Sector. Among them, the works of Floquet (1998) and

Gräfe (1999) in the Outer Navarro-Cantabrian Platform and the North-Castilian Sector, and of Alonso *et al* . (1993) and Segura *et al*. (1999) in the Central Sector, stood out by their exhaustivity and acceptation.

2.2. Western Portuguese Carbonate Platform

In Portugal, early research on palaeontology and stratigraphy is dated from the middle 19th century (Sharpe, 1849) and had continuity with subsequent contributions (among them those by Choffat, 1886, 1898, 1900, 1901-02) that described the Cretaceous of West Central Portugal, including the regions of Beira Litoral (Figueira da Foz to Coimbra and Aveiro) and Estremadura (Lisbon to Nazaré and Leiria), with emphasis on the Cenomanian and Turonian stages and main palaeontological groups. After these first decades of fruitful research, more than half a century elapsed till the stratigraphy and palaeontology of the Baixo Mondego was reviewed by Ferreira Soares (1966, 1972, 1980). These works were followed by biostratigraphic studies undertaken by Lauverjat (1982) and Berthou (1984), among others.

Since 1992, the Cenomanian and lower Turonian cephalopod faunas of West Central Portugal have been extensively reviewed, with emphasis on systematics and biostratigraphy (Callapez, 1992, 1998, 2003, 2004, 2008; Callapez and Ferreira Soares, 2001; Callapez *in* Hart *et al*., 2005). These studies have been based on a new reference collection assembled at the University of Coimbra (with species inedit to the Lusitanian area), and the Choffat Collection of the Geological Survey, making it possible for the first time, to establish an integrated biostratigraphy with other areas of the Tethyan Realm.

3. Geological setting

The studied Spanish outcrops form part of a large northwest-to-southeast orientated band constituted by a thick carbonate sedimentary sequence (limestones and marlstones), with some interbedded terrigenous and dolostone intervals. Their cephalopods have been mainly collected from the Margas de Puentedey (Floquet *et al*., 1982) and Margas de Picofrentes (Floquet *et al*., 1982) formations, deposited in the inner and the marginal environments of the platform, respectively. The studied Portuguese exposures are part of a band of Upper Cretaceous carbonate platform that outcrops across the northern margin of the Baixo Mondego, from Coimbra to Figueira da Foz. To the south there is a related set of outcrops orientated along the southern block of the northeast-southwest tectonic and diapiric axis of Nazaré-Leiria-Pombal.

During the Late Cretaceous, the current Iberian Peninsula was a relatively independent tectonic unit, called Iberian Subplate. The combined incidence of the eustatic worldwide changes and the local tectonic readjustments generated several faunal turnovers and depositional sequences in the epicontinental flooded regions of the Iberian Subplate, among those the Iberian Trough and the Western Portuguese Platform (Text-fig. 2).

Specifically, the Iberian Trough (IT) was a long, narrow and relatively stable intracratonic ramp, and comprised the northern, central and south-eastern regions of the Iberian Subplate that were temporally or permanently flooded by the Protoatlantic Ocean, the Tethys Sea or both. It was bordered on the west by the Hesperian Massif and on the east by the Ebro Massif, and was broadly related to the North Cantabrian, Basque, Pyrenean and Levantine basins. The IT was divided into different domains. These were, from the north to the southeast, the Outer Navarro-Cantabrian Platform, the Inner Castilian Platform and the Levantine Platform. The Inner Castilian Platform was divided into the North-Castilian Sector and the Central Sector. The North-Castilian Sector included the North-Ebro Area and the South-Ebro Area, and the Central Sector comprised the La Demanda Area and the Guadarrama Area. Further readings about the main subjects related with the geological evolution of the IT were given by Amiot (1982), Floquet *et al*. (1982), Rosales *et al*. (2002), Mas *et al*. (2002), Floquet (2004) and García *et al*. (2004).

The Western Portuguese Carbonate Platform (WPCP) included the central-western regions of the Iberian Subplate, and was broadly related with the Atlantic Lusitanic Basin (Ferreira Soares and Rocha, 1985). It experienced a complex tectonic control with reactivated late Hercynian faults and halokinetic structures, and at least three main rifting phases intercalated with intervals of post-rift thermal subsidence (Wilson *et al*., 1989; Hiscott, 1990). The tectono-sedimentary evolution of this basin enabled the formation of a relatively homogeneous and stable basal upper Cenomanian carbonate platform with cephalopods. Subsequently, a clear differentiation on the palaeogeographic setting of this carbonate platform was established, with ammonites restrained to the Baixo Mondego, and a large domain of shoals with coral and rudist fringes developed southwards in Leiria and Nazaré. Further readings about the main subjects related with the stratigraphy of the WPCP can be consulted in Ferreira Soares (1980), Lauverjat (1982), Berthou (1984), Callapez (1998, 2004, 2008), Hart *et al*., (2005) and Rey *et al*. (2006).

In the present paper, the palaeogeographical division and the ammonite zonation for the upper Cenomanian and

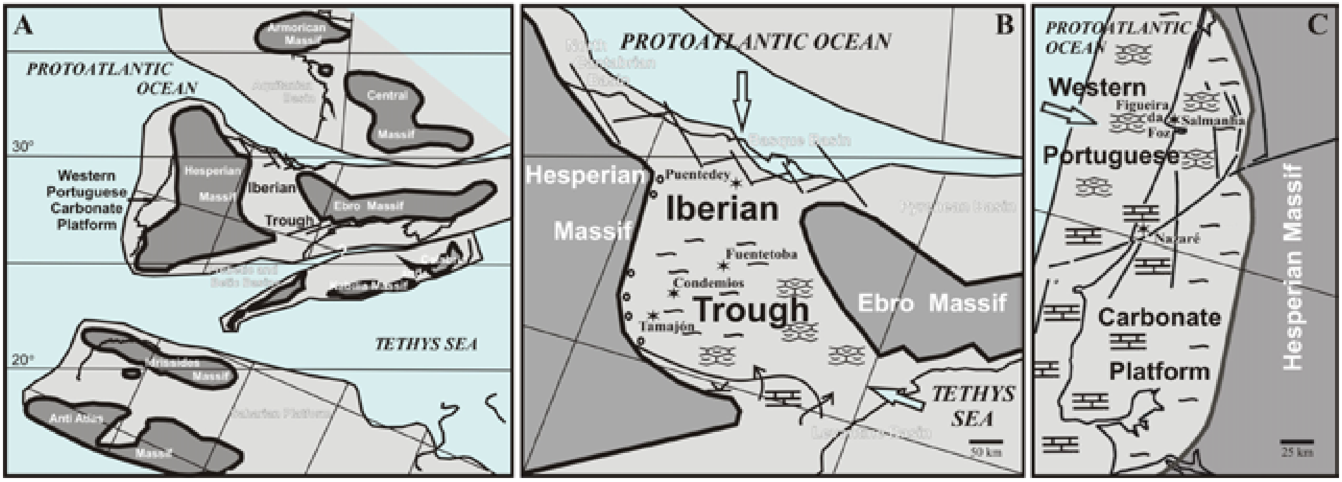


Fig. 2.- Palaeogeographic general situation of the Iberian Peninsula during the maximum transgression of the late Cenomanian-Early Turonian (A), with the approximate locations of the main Spanish (B) and Portuguese (C) studied outcrops and the facies distribution. Modified from Philip and Floquet (2000), Stampfli *et al*. (2001) and Gelabert *et al*. (2002). The circles symbolize coastal terrigenous, the horizontal rectangles indicate the position of relatively shallow water carbonate platform sediments, the curved lines stand for the marls deposited in deeper regions of the platform, and the hexagons represent bioclastic limestones located in intermediate bathymetries.

Fig. 2.- Situación paleogeográfica general de la Península Ibérica durante el máximo transgresivo del Cenomaniense superior-Turoniense inferior (A), con la localización de las principales secciones españolas (B) y portuguesas (C) estudiadas y la distribución de facies. Modificado de Philip y Floquet (2000), Stampfli *et al*. (2001) y Gelabert *et al*. (2002). Los círculos simbolizan depósitos terrígenos costeros, los rectángulos horizontales carbonatos someros, las líneas onduladas margas más profundas y los hexágonos calizas bioclásticas de batimetrías intermedias.

lower Turonian of the IT proposed by Barroso-Barcenilla *et al*. (2009) and of the WPCP developed by Callapez and Ferreira Soares (2001) and Callapez (2003, 2008) have been followed. These zonal schemes, on the basis of the occurrence of the index species, have been correlated between them and with that of the type-section of Pueblo, USA, and with those zonations that can be considered as representative of the Boreal (Western Europe) and Tethyan (North Africa) domains (Text-fig. 3). The interregional correlations presented herein have been made according to the conclusions of Graciansky *et al*. (1998).

4. Cephalopod assemblages

The main part of the cephalopods collected in the upper Cenomanian and the lower Turonian of the IT (Barroso-Barcenilla, 2006, 2007; Barroso-Barcenilla and Goy, 2007, 2009, 2010; Barroso-Barcenilla *et al*., 2009) and the WPCP (Callapez, 1998, 2003; Callapez and Ferreira Soares, 2001) do not present signs of taphonomic resedimentation or reelaboration (*sensu* Fernández-López, 2000), and the few that show any of these signs do not seem to have suffered notable alterations. Therefore, it can be considered that all of them maintain their respective original stratigraphic positions (Callapez, 1998; Barroso-Barcenilla, 2006). The comparison and integration of the successions and co-occurrences of these cephalopods has allowed us to differentiate nine cephalopod assemblages within the materials of this interval, which have been numbered in stratigraphic ascending order (Text-fig. 4).

These assemblages (1 to 9) own notably different taxa and can be related to certain palaeoecologic turnovers that happened in the studied basins, both with external origin or due to local tectonic and palaeogeographical changes. Each of them has been interpreted considering the narrow relation that was established in the epicontinental platforms between the palaeoecologic changes and the general palaeontological record, emphasized by Fernández-Lopez (1999, 2000), or the specific succession of cephalopods, studied by Hirano *et al*. (2000) and Toshimitsu and Hirano (2000), among others. These authors maintain that the ammonoid diversity was primarily controlled by changes in the marine environments. On this basis, several eustatic, tectonic or geochemical alterations have been inferred, which concerned the habitability of the region during the considered interval, providing interesting information about the evolution of the Iberian Subplate.

4.1. Assemblage 1

This assemblage can be recognized overlaying the stratigraphic discontinuity of the middle-upper Cenomanian boundary, in the *Eucalycoceras rowei* zone of the IT, and includes the co-occurrence of *Eucalycoceras* with *Calycoceras*. In it, the taxa *Eucalycoceras rowei*, *Calycoceras* (*Proeucalycoceras*) sp., *Calycoceras* (*Calycoceras*) sp. and, seemingly, *Calycoceras* (*Calycoceras*) *naviculare*, have been identified, all of them belonging to the Acanthoceratidae. In the WPCP its lower part corresponds to a stratigraphic interval with the bivalve *Gyrostrea ouremensis*, but without known ammonites. The materials in which this assemblage has been recorded reach a restricted geographic distribution (exclusively the IT) and only own cephalopods moderately adapted to shallow marine environments (*Eucalycoceras* and *Calycoceras*: Batt, 1989; Westermann, 1996). In the same way, it can be added that both the number and the diversity of the collected specimens are relatively scarce (3 or 4 species).

4.2 Assemblage 2

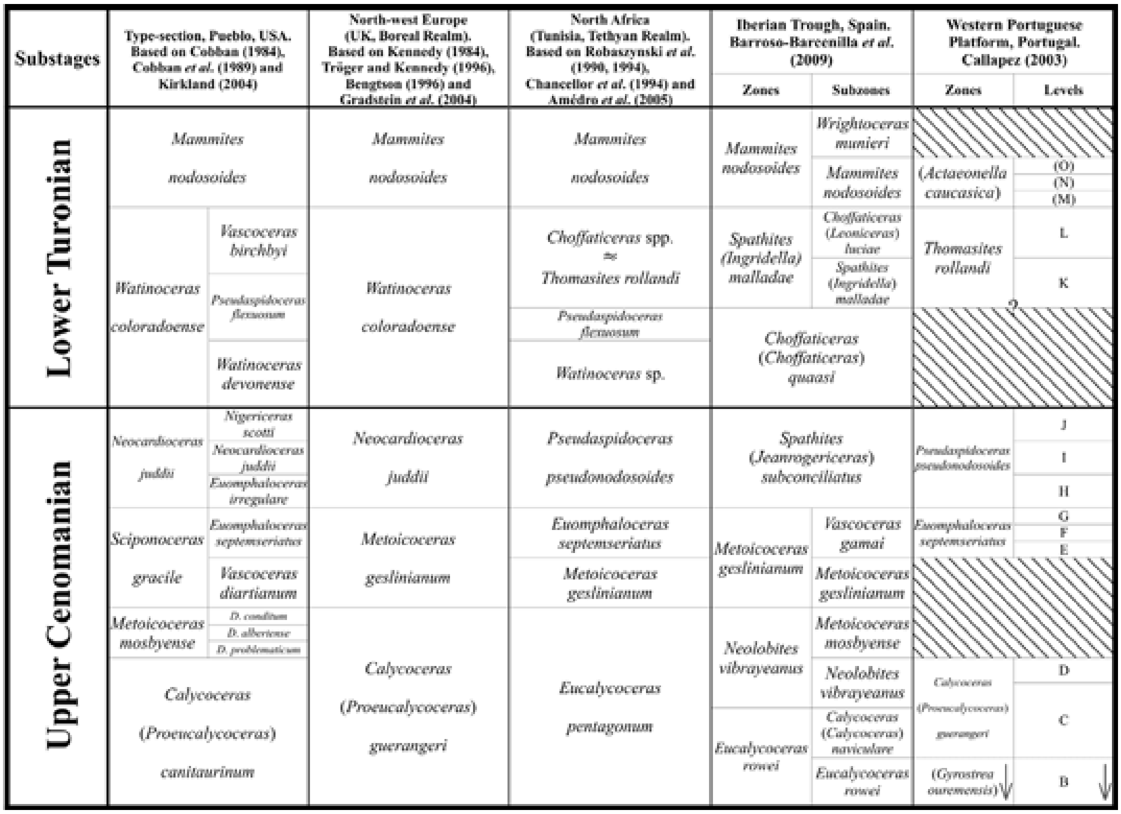
It is recorded in the upper Cenomanian *Neolobites vibrayeanus* subzone of the IT and the *Calycoceras* (*Eucalycoceras*) *guerangeri* zone of the WPCP, and includes the co-occurrence of *Angulithes* with *Neolobites*, in the Nautilidae and Engonoceratidae in both basins, and of *Euomphaloceras* with *Calycoceras*, in the Acanthoceratidae in the former, and of *Calycoceras*, in the same family, in the latter. In it, the following taxa have been recognized: *Angulithes mermeti*, *Neolobites vibrayeanus* and *Calycoceras* (*Calycoceras*) *naviculare*, in both basins; *Lotzeites* sp. and *Euomphaloceras euomphalum*, in the IT; and *Neolobites bussoni*, *Calycoceras* (*Proeucalycoceras*) *guerangeri*, *Eucalycoceras pentagonum*, *Thomelites hancocki* and *Puzosia* (*Parapuzosia*) sp., in the WPCP. In this interval, it can be observed a notable increase in the number of localities that yielded fossil cephalopods, as well as in the diversity of these invertebrates (10 species). Among them, the abundance of *Angulithes* and *Neolobites* stand out, initially typical of relatively deep or open waters, and there is a near absence of taxa characteristic of epicontinental environments. The co-occurrence of *Angulithes* and *Neolobites* in this interval has been observed by different authors in other basins (Peru: Benavides-Cáceres, 1956; Morocco: Meister and Rhalmi, 2002, Cavin *et al*., 2010).

4.3. Assemblage 3

It can be recognized in the upper Cenomanian *Metoicoceras mosbyense* and *Metoicoceras geslinianum* subzones of the IT, where includes the co-occurrence of *Metoicoceras*, and only owns the species *Metoicoceras mosbyense* and *Metoicoceras geslinianum*, of the Acanthoceratidae. Although it can be identified across a relatively high number of localities of the IT, its taxonomic diversity is very low (2 species). Nevertheless, it is within this assemblage that the first phylogenetic line between two species of cephalopods (*M. mosbyense* and *M. geslinianum*) can be established in the upper Cenomanian of the Iberian Subplate. Also, it seems to be especially significant the fact that, as revealed by geochemical analyses realized in collaboration with the Prof. Dr. W.J. Kennedy in the Puentedey Section, the materials corresponding to the *M. geslinianum* subzone registered the first and punctual of the two positive excursions of the δC^{13} signal (the second and main in the *S.* (*J.*) *subconciliatus* zone), seemingly related with the Ocean Anoxic Event of the Cenomanian-Turonian Transition (OAE2) of Schlanger and Jenkyns (1976) (Barroso-Barcenilla *et al*., 2011). Similar isotopic variations were observed by other authors, such as Kennedy *et al*. (2000) and Caron *et al*. (2006) in correlative levels of other regions and, thus, they were possibly produced by worldwide oceanographic and climatic changes.

4.4. Assemblage 4

This important set has been registered in the upper Cenomanian *Vascoceras gamai* subzone and the *Spathites* (*Jeanrogericeras*) *subconciliatus* zone of the IT, and the *Euomphaloceras septemseriatus* and the *Pseudaspidoceras pseudonodosoides* zones of the WPCP. It includes, in the IT, the co-occurrence of *Vascoceras* 1 (*sensu* Barroso-Barcenilla, 2006), in the Vascoceratidae, and of *Spathites* (*Jeanrogericeras*) 1 (*sensu* Barroso-Barcenilla, 2006), in the Acanthoceratidae, and, in the WPCP, the co-occurrence of *Vascoceras* 1 with *Rubroceras*, in the Vascoceratidae, and of *Euomphaloceras* with *Pseudocalycoceras* and of *Spathites* (*Jeanrogericeras*) 1 with *Pseudaspidoceras*, in the Acanthoceratidae. In this assemblage, the following taxa have been recognized: *Vascoceras gamai*, *Vascoceras barcoicense*, *Fagesia catinus* and *Spathites* (*Jeanrogericeras*) *subconciliatus*, in both basins; *Vascoceras charoni*, *Vascoceras durandi*, *Vascoceras cauvini*, *Spathites* (*Jeanrogericeras*) *robustus* and *Parapuzosia* (*Austiniceras*) sp., in the IT; and *Pseudocalycoceras* sp., *Euomphaloceras septemseriatus*, *Vascoceras adonense*, *Vascoceras silvanense*, *Vascoceras* sp., *Vascoceras douvillei*, *Vascoceras kossmati*, *Rubroceras* cf. *alatum*, *Rubroceras* sp., *Pseudaspidoceras pseudonodosoides*, *Puzosia* (*Puzosia*) sp. and *Pachydesmoceras denisonianum*, in the WPCP. It records the early arrival of vascoceratid ammonites to the Iberian Subplate, and reveals a domi-



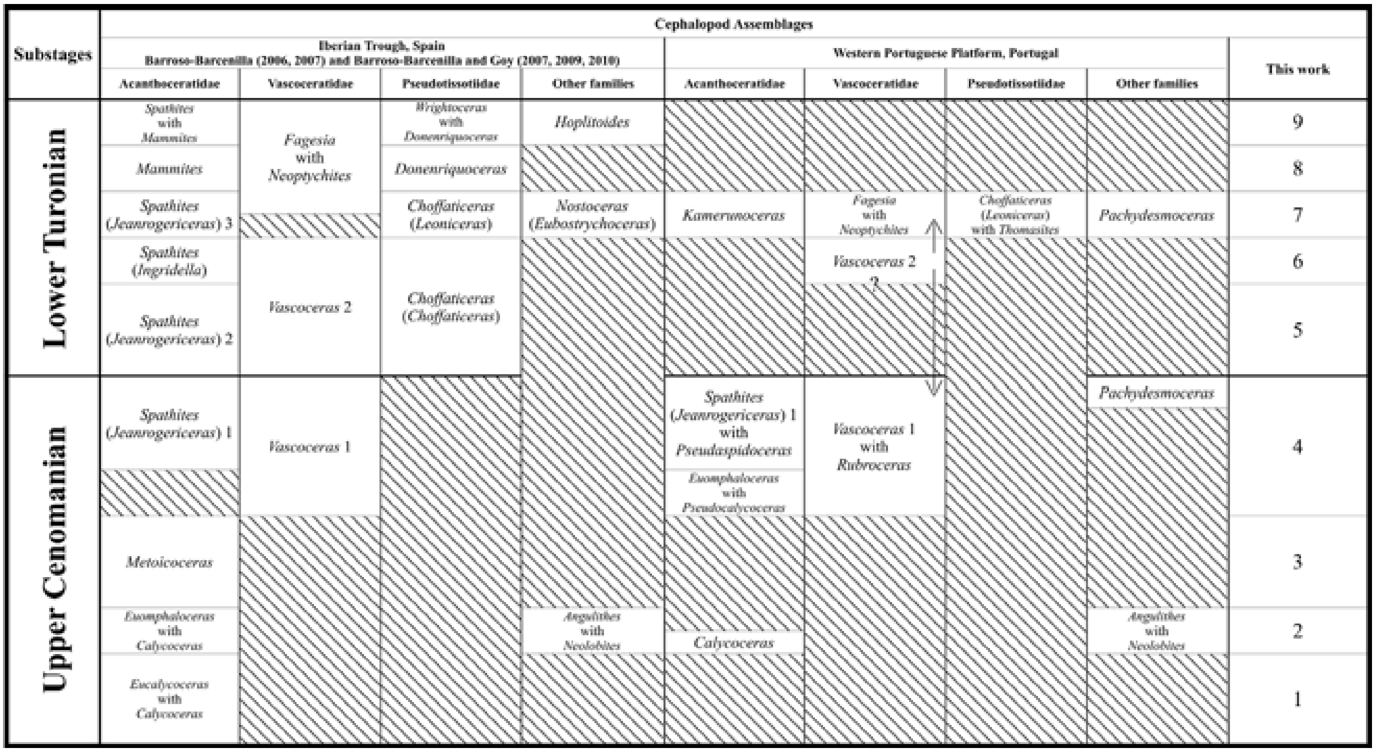
Substages	Type-section, Pueblo, USA. Based on Cobban (1984), Cobban *et al.* (1989) and Kirkland (2004)		North-west Europe (UK, Boreal Realm). Based on Kennedy (1984), Tröger and Kennedy (1996), Bengtson (1996) and Gradstein *et al.* (2004)	North Africa (Tunisia, Tethyan Realm). Based on Robaszynski *et al.* (1990, 1994), Chancellor *et al.* (1994) and Amédro *et al.* (2005)	Iberian Trough, Spain. Barroso-Barcenilla *et al.* (2009)		Western Portuguese Platform, Portugal. Callapez (2003)	
					Zones	Subzones	Zones	Levels
Lower Turonian	*Mammites nodosoides*		*Mammites nodosoides*	*Mammites nodosoides*	*Mammites nodosoides*	*Wrightoceras munieri*	▨	▨
						Mammites nodosoides	(*Actaeonella caucasica*)	(O)
								(N)
								(M)
	Watinoceras coloradoense	*Vascoceras birchbyi*	*Watinoceras coloradoense*	*Choffaticeras* spp. ≈ *Thomasites rollandi*	*Spathites* (*Ingridella*) *malladae*	*Choffaticeras* (*Leoniceras*) *luciae*	*Thomasites rollandi*	L
						Spathites (*Ingridella*) *malladae*		K ?
		Pseudaspidoceras flexuosum		*Pseudaspidoceras flexuosum*	*Choffaticeras* (*Choffaticeras*) *quaasi*		▨	▨
		Watinoceras devonense		*Watinoceras* sp.				
Upper Cenomanian	*Neocardioceras juddi*	*Nigericeras scotti*	*Neocardioceras juddi*	*Pseudaspidoceras pseudonodosoides*	*Spathites* (*Jeanrogericeras*) *subconciliatus*		*Pseudaspidoceras pseudonodosoides*	J
		Neocardioceras juddi						I
		Euomphaloceras irregulare						H
	Sciponoceras gracile	*Euomphaloceras septemseriatus*	*Metoicoceras geslinianum*	*Euomphaloceras septemseriatus*	*Metoicoceras geslinianum*	*Vascoceras gamai*	*Euomphaloceras septemseriatus*	G
								F
								E
		Vascoceras diartianum		*Metoicoceras geslinianum*		*Metoicoceras geslinianum*	▨	▨
	Metoicoceras mosbyense	*D. conditum*	*Calycoceras* (*Proeucalycoceras*) *guerangeri*	*Eucalycoceras pentagonum*	*Neolobites vibrayeanus*	*Metoicoceras mosbyense*		
		D. albertense						
		D. problematicum						
	Calycoceras (*Proeucalycoceras*) *canitaurinum*					*Neolobites vibrayeanus*	*Calycoceras* (*Proeucalycoceras*) *guerangeri*	D
					Eucalycoceras rowei	*Calycoceras* (*Calycoceras*) *naviculare*		C
						Eucalycoceras rowei	(*Gyrostrea ouremensis*) ↓	B ↓

Fig. 3.- Possible correlation of the biostratigraphic zonations used for the Iberian Trough and the Western Portuguese Carbonate Platform with other scales. For interregional correlations, the work of Graciansky *et al.* (1998) has been especially useful. The oblique lines indicate interval without record, and the arrows represent that the zone or level continues. *D. problematicum* is *Dunveganoceras problematicum*, *D. albertense* is *Dunveganoceras albertense* and *D. conditum* is *Dunveganoceras conditum*. *Gyrostrea ouremensis* and *Actaeonella caucasica* zones are in brackets because their index species are not ammonites. M, N and O levels are in brackets because, to date, they have not provided ammonites.

Fig. 3.- Posible correlación de las zonaciones bioestratigráficas utilizadas en el Surco Ibérico y la Plataforma Carbonatada Occidental Portuguesa con otras escalas. Para correlaciones interregionales ha sido especialmente útil el trabajo de Graciansky *et al.* (1998). Las líneas oblicuas indican intervalo sin registro, y las flechas representan que la zona o el nivel continúa. *D. problematicum* es *Dunveganoceras problematicum*, *D. albertense* es *Dunveganoceras albertense* y *D. conditum* es *Dunveganoceras conditum*. Las zonas *Gyrostrea ouremensis* y *Actaeonella caucasica* están entre paréntesis porque sus especies índice no son ammonites. Los niveles M, N y O están entre paréntesis porque, hasta ahora, no han proporcionado ammonites.

nant influence of Tethyan *warm guests* on the marine invertebrate faunas, as advanced by Wiedmann, 1975b.

This is a notably complex main assemblage with numerous taxa of diverse affinities and influenced by significant and global phenomena of hypoxia of the OAE2 which can be divided into two consecutive minor intervals. The first one (4_1) can be recognized in the *Vascoceras gamai* subzone of the IT and the *Euomphaloceras septemseriatus* zone of the WPCP, and is notably better represented in the WPCP. In it, the cephalopod diversity is low (4 species), as only *V. gamai* (one of the *Vascoceras* with wider geographical distribution) has been identified in restricted areas of the IT, and the same species, *Puzosia* (*P.*) sp., *Pseudocalycoceras* sp. and *E. septemseriatus* have been collected in the WPCP. The second interval (4_2) has been registered in the *Spathites* (*Jeanrogericeras*) *subconciliatus* zone of the IT, and the *Pseudaspidoceras pseudonodosoides* zone of the WPCP, and is partly contemporaneous to the second and main of the two positive excursions of the δC^{13} signal related with the OAE2 (Barroso-Barcenilla *et al*., 2011). In it, initially (1st) the ammonite diversity increases (10 species), with several representatives of *Vascoceras* in the Guadarrama Area and in the WPCP; the first members of *Spathites* (*Jeanrogericeras*), specifically *S.* (*J.*) *subconciliatus*, in both basins; and the first representatives of *Pseudaspidoceras* and *Rubroceras*, specifically *P. pseudonodosoides*, *R.* cf. *alatum* and *R.* sp., in the WPCP, all of them with geographic distributions narrower than *V. gamai*. It continues (2nd) with the presence of the dark



Substages	Cephalopod Assemblages								This work
	Iberian Trough, Spain Barroso-Barcenilla (2006, 2007) and Barroso-Barcenilla and Goy (2007, 2009, 2010)				Western Portuguese Platform, Portugal				
	Acanthoceratidae	Vascoceratidae	Pseudotissotiidae	Other families	Acanthoceratidae	Vascoceratidae	Pseudotissotiidae	Other families	
Lower Turonian	*Spathites* with *Mammites*	*Fagesia* with *Neoptychites*	*Wrightoceras* with *Donenriquoceras*	*Hoplitoides*	▨	▨	▨	▨	9
	Mammites		*Donenriquoceras*	▨					8
	Spathites (*Jeanrogericeras*) 3	▨	*Choffaticeras* (*Leoniceras*)	*Nostoceras* (*Eubostrychoceras*)	*Kamerunoceras*	*Fagesia* with *Neoptychites*	*Choffaticeras* (*Leoniceras*) with *Thomasites*	*Pachydesmoceras*	7
	Spathites (*Ingridella*)	*Vascoceras* 2	*Choffaticeras* (*Choffaticeras*)	▨	▨	*Vascoceras* 2 ?	▨	▨	6
	Spathites (*Jeanrogericeras*) 2					▨			5
Upper Cenomanian	*Spathites* (*Jeanrogericeras*) 1 ▨	*Vascoceras* 1	▨		*Spathites* (*Jeanrogericeras*) 1 with *Pseudaspidoceras* *Euomphaloceras* with *Pseudocalycoceras*	*Vascoceras* 1 with *Rubroceras*		*Pachydesmoceras* ▨	4
	Metoicoceras	▨			▨	▨			3
	Euomphaloceras with *Calycoceras*			*Angulithes* with *Neolobites*	*Calycoceras*			*Angulithes* with *Neolobites*	2
	Eucalycoceras with *Calycoceras*			▨	▨			▨	1

Fig. 4.- Cephalopod assemblages identified in the Iberian Trough and the Western Portuguese Carbonate Platform. The oblique lines indicate interval without record, and the arrows represent that the assemblage continues.

Fig. 4.- Asociaciones de cefalópodos identificadas en el Surco Ibérico y la Plataforma Carbonatada Occidental Portuguesa. Las líneas oblicuas indican intervalo sin registro, y las flechas representan que la asociación continúa.

levels of the second and main phase of the OAE2 in the North-Ebro Area (Puentedey, Barroso-Barcenilla *et al*., 2011), together with numerous and almost monospecific levels with *S*. (*J*.) *subconciliatus* in the whole IT, as well as a widespread marly-dolomitic sequence with spatangoids and cephalopods in the WPCP stand out. In them, the cephalopod diversity is much lower (2 species), and besides *S*. (*J*.) *subconciliatus*, only *V*. *durandi* has been identified, specifically in the Guadarrama Area (Tamajón: Barroso-Barcenilla *et al*., 2009). The deposition of hypoxic sediments in deep environments of the IT was studied by several authors, such as Paul *et al*. (1994) and Rodríguez-Lázaro *et al*. (1998), and recently confirmed by the geochemical analyses developed in the Puentedey Section by Barroso-Barcenilla *et al*. (2011). The practically exclusive presence of a species of cephalopod that shows a wide morphologic variability in a biostratigraphic interval, like in case of *S*. (*J*.) *subconciliatus* in a part of the homonymous zone, was observed by different researchers, such as Meister *et al*. (1992). Finally (3rd), the cephalopod diversity increases notably (11 species), having registered representatives of *S*. (*Jeanrogericeras*), *Fagesia*, *P*. (*Austiniceras*), *P*. (*Puzosia*) and *Pachydesmoceras* and, mainly of *Vascoceras*, some of them belonging to exotic species.

4.5. Assemblage 5

It is recorded in the lower Turonian *Choffaticeras* (*Choffaticeras*) *quaasi* zone of the IT, and includes the co-occurrence of *Spathites* (*Jeanrogericeras*) 2 (*sensu* Barroso-Barcenilla, 2006), in the Acanthoceratidae, and the first interval of the co-occurrence of *Vascoceras* 2 (*sensu* Barroso-Barcenilla, 2006), in the Vascoceratidae, and of *Choffaticeras* (*Choffaticeras*), in the Pseudotissotiidae, with the species *Spathites* (*Jeanrogericeras*) *subconciliatus*, *Spathites* (*Jeanrogericeras*) *tavense*, *Spathites* (*Jeanrogericeras*) *saenzi*, *Spathites* (*Jeanrogericeras*) *postsaenzi*, *Vascoceras durandi*, *Vascoceras amieirense*, *Vascoceras harttii*, *Choffaticeras* (*Choffaticeras*) *quaasi*, *Choffaticeras* (*Choffaticeras*) *pavillieri* and, possibly, *Pseudotissotia* sp. This assemblage has not been recognised in the sedimentary record of WPCP. Its taxonomic diversity is very high (9 or 10 species) and, in it, phylogenetic relationships can be established between almost all the represented species (Acanthoceratidae: Barroso-Barcenilla, 2007; Vascoceratidae: Barroso-Barcenilla and Goy, 2009, 2010; Pseudotissotiidae: Barroso-Barcenilla and Goy, 2007). Although the two endemics *S*. (*J*.) *saenzi* and *S*. (*J*.) *postsaenzi* exist in the same, the groups from the Tethys, such as the vascoceratids and the pseudotissotiids (Meister *et al*., 1994; Courville *et al*., 1998), clearly predominate.

4.6. Assemblage 6

It is typical of the lower Turonian *Spathites* (*Ingridella*) *malladae* subzone of the IT, and includes the co-occurrence of *Spathites* (*Ingridella*), in the Acanthoceratidae, and the second interval of the co-occurrence of *Vascoceras* 2 and of *Choffaticeras* (*Choffaticeras*). In it, the following species have been identified: *Spathites* (*Ingridella*) *malladae*, *Spathites* (*Jeanrogericeras*) *obliquus*, *Spathites* (*Jeanrogericeras*) *reveliereanus*, *Kamerunoceras ganuzai*, *Vascoceras amieirense*, *Vascoceras harttii*, *Vascoceras kossmati*, *Choffaticeras* (*Choffaticeras*) *pavillieri*, *Choffaticeras* (*Choffaticeras*) *sinaiticum*, *Wrightoceras llarenai*, *Angulithes vascogoticus* and, possibly, *Choffaticeras* (*Choffaticeras*) *segne*. It could also be partly correlative to the K level of the WPCP, which includes the co-occurrence of *Vascoceras* 2 and of *Choffaticeras* (*Choffaticeras*) just below a diverse fauna from the *Thomasites rollandi* zone. In this dolomitic unit of the WPCP, which yielded a very scarce fauna of bivalves (*Mytiloides*) and ammonites, the species *Vascoceras kossmati*, *Vascoceras durandi* and, possibly, *Pachydesmoceras denisonianum* have been identified. In assemblage 6, although the ammonite diversity become extraordinarily high (11 or 12 species), the increase on the proportion of taxa almost exclusively from the Iberian Subplate (Wright, 1996; Barroso-Barcenilla and Goy, 2007) is very relevant. Among these, the subgenus *Spathites* (*Ingridella*) stands out for its higher relative abundance.

4.7. Assemblage 7

It can be recognized in the lower Turonian *Choffaticeras* (*Leoniceras*) *luciae* subzone of the IT, and the L level of the *Thomasites rollandi* zone of the WPCP, and includes the co-occurrence of *Spathites* (*Jeanrogericeras*) 3 (*sensu* Barroso-Barcenilla, 2006), in the Acanthoceratidae, of *Choffaticeras* (*Leoniceras*), in the Pseudotissotiidae, and of *Nostoceras* (*Eubostrychoceras*), in the Nostoceratidae, in the former region, and of *Kamerunoceras*, in the Acanthoceratidae, of *Fagesia* with *Neoptychites*, in the Vascoceratidae, of *Choffaticeras* (*Leoniceras*) with *Thomasites*, in the Pseudotissotiidae, and of *Pachydesmoceras*, in the Desmoceratidae, in the latter region. In it, the following taxa have been identified: *Spathites* (*Jeanrogericeras*) *reveliereanus*, *Choffaticeras* (*Leoniceras*) *luciae*, *Choffaticeras* (*Leoniceras*) *barjonai* and *Nostoceras* (*Eubostrychoceras*) sp., in the IT, and *Kamerunoceras douvillei*, *Vascoceras kossmati*, *Vascoceras durandi*, *Fagesia tevesthensis*, *Fagesia superstes*, *Neoptychites cephalotus*, *Thomasites rollandi*, *Choffaticeras* (*Leoniceras*) *barjonai*, *Pachydesmoceras denisonianum* and *Parapuzosia* (*Austiniceras*) *intermedia orientalis*, in the WPCP. In this assemblage, fully recognised in both Spanish and Portuguese lower Turonian successions, the diversity is relatively higher (14 species). Nevertheless, each of the identified families is represented by a single species, with the only exception of Pseudotissotiidae. Within this family, a progressive replacement of *Ch*. (*L*.) *luciae* by *Ch*. (*L*.) *barjonai* seems to be observed, since the latter species presents, at least in the IT, a slightly higher range than the former. Likewise, the near absence of taxa from shallow environments stands out, since the majority of the identified forms were from open or relatively deep waters, such as the oxycone *Choffaticeras* (*Leoniceras*) and the torticone *Nostoceras* (*Eubostrychoceras*) (Batt, 1989; Westermann, 1996).

Within the highest interval recorded from the levels where this assemblage has been identified, *Fagesia tevesthensis* has been recognized. For this reason, although it can be a mere effect of the sampling detail, the lower part of the assemblage of *Fagesia* with *Neoptychites*, in the Vascoceratidae, has been placed inside the same one.

4.8. Assemblage 8

It is recorded in the lower Turonian *Mammites nodosoides* subzone of the IT, and includes the co-occurrence of *Mammites*, in the Acanthoceratidae, of *Donenriquoceras*, in the Pseudotissotiidae, and the middle part of *Fagesia* with *Neoptychites*, with the species *Mammites nodosoides*, *Spathites* (*Jeanrogericeras*) *reveliereanus*, *Fagesia tevesthensis*, *Fagesia rudra*, *Fagesia mortzestus*, *Fagesia superstes*, *Neoptychites cephalotus*, *Donenriquoceras forbesiceratiforme* and *Pachydesmoceras linderi*. In the WPCP it corresponds to a stratigraphic interval with gastropods of the species *Actaeonella caucasica* and of the group of the nerineids, but without ammonites. Inside its notable diversity (9 species), the groups proceeding from the Protoatlantic stand out, such as *Mammites* and *Fagesia* (Wiedmann, 1975b; Kennedy and Cobban, 1976), but those from relatively open and deep environments, such as *Neoptychites* (Batt, 1989; Westermann, 1996), and the endemics, such as *Donenriquoceras* (Wright, 1996; Barroso-Barcenilla and Goy, 2007), are also represented.

4.9. Assemblage 9

It can be recognized in the lower Turonian *Wrightoceras munieri* subzone of the IT, and includes the co-occurrence of *Spathites* with *Mammites*, in the Acanthoceratidae, of *Wrightoceras* with *Donenriquoceras*, in the Pseudotissotiidae, of *Hoplitoides*, in the Coilopoceratidae, and the upper part of *Fagesia* with *Neoptychites*, with the species *Spathites* (*Jeanrogericeras*) *obliquus*, *Spathites* (*Jeanrogericeras*) *reveliereanus*, *Spathites* (*Jeanrogericeras*) *combesi*, *Spathites* (*Ingridella*) *depressus*, *Spathites* (*Spathites*) *laevis*, *Spathites* (*Spathites*) *sulcatus*, *Mammites nodosoides*, *Fagesia superstes*, *Neoptychites cephalotus*, *Wrightoceras munieri*, *Donenriquoceras forbesiceratiforme* and *Hoplitoides ingens*. In it, the taxonomic diversity is comparatively high (12 species), and among the represented forms the endemic ones stand out, such as *S*. (*J*.) *obliquus*, *S*. (*I*.) *depressus* and *S*. (*S*.) *sulcatus* (Santamaría-Zabala, 1995; Barroso-Barcenilla 2007), together with those which seem to have arisen by means of processes more or less marked of adaptation to the platform palaeoenvironments, such as *S*. (*J*.) *combesi* and *F*. *superstes* (Batt, 1989; Westermann, 1996).

5. Depositional sequences

Both the IT and WPCP sedimentary successions of the studied interval were deposited during the course of two 3rd order depositional sequences, known by Haq *et al*. (1988) as UZA-2.4 and UZA-2.5, respectively.

In the IT, the first one of them, named DC-5 by Floquet (1998), UC-4/5 by Gräfe (1999), DS-5 by Alonso *et al*. (1993) and S-3 by Segura *et al*. (1999), includes the basal and middle upper Cenomanian. The second sequence extends from the higher upper Cenomanian to the middle Turonian. In detail, in the north of the IT (Outer Navarro-Cantabrian Platform and North-Castilian Sector), within this second sequence, two other lower order sequences can be differentiated, called DC-6a and DC-6b by Floquet (1998), and UC-5/6 and UC-6/7 by Gräfe (1999), respectively. However, these two intervals can not be individualized in the centre of the IT (Central Sector), but are coincident with the lower and middle part of the sequence DS-6 of Alonso *et al*. (1993) and with the sequence S-4 of Segura *et al*. (1999), and present a more diffuse upper boundary. These differences between the sequences of the north and the centre of the IT can be caused, in part, by the inequality of records of both areas.

In the WPCT, and despite a perceptible influence of local tectonics over the eustatic signature, the same sequences of the IT can be correlated with the 3rd order depositional sequences and subsequent sequences defined by Callapez (1998). In particular, the Portuguese sequence CD records part of the depositional sequence A proposed on this work; sequences E/I and J match with the lower half of B_1, and K/L and M/O with B_2 (Text-fig. 5).

There is an obvious relationship between these two major depositional sequences and the nine cephalopod assemblages described above in the Iberian Subplate. The first of these sequences, which have been named A, can be related to the assemblages 1 to 3, and the second one, called B, to 4 to 9. Each of these depositional sequences includes different genera of cephalopods and coincides with specific worldwide 3rd order eustatic cycles observed by Haq *et al.* (1988), and certain depositional sequences recognized in the IT by numerous authors, as Floquet (1998), Gräfe (1999), Alonso *et al*. (1993) and Segura *et al*. (1999). In the same way, inside the second major sequence, two minor depositional sequences have been differentiated, named B_1 and B_2, which group, respectively, 4 to 6 and 7 to 9 assemblages, and which agree with some specific sequences of Floquet (1998) and Gräfe (1999), among others. All these sequences, both major and minor, can be assimilated to the palaeontological cycles defined by Fernandez-Lopez (2000).

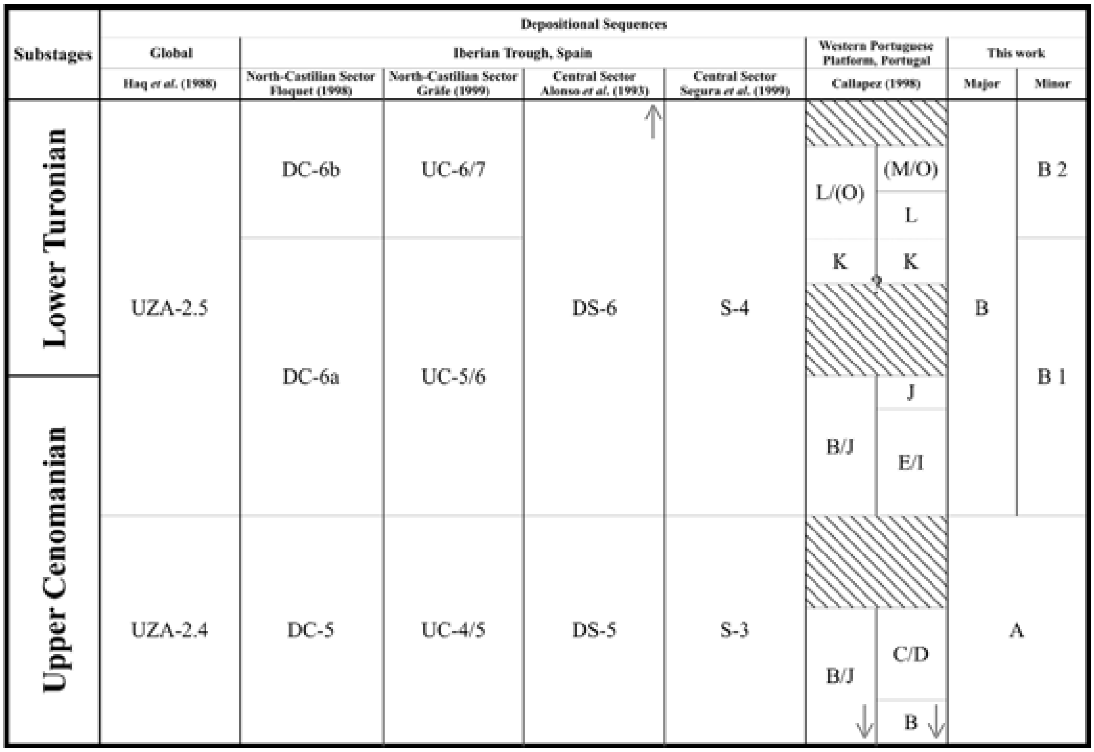
5.1. Sequence A

It is seemingly related to the 3rd order depositional sequence UZA-2.4 of Haq *et al*. (1988) and the sequences DC-5 of Floquet (1998), UC-4/5 of Gräfe (1999), DS-5 of Alonso *et al*. (1993) and S-3 of Segura *et al*. (1999). It shows an extensive record that ranges from the base of the upper Cenomanian to the top of the *Metoicoceras geslinianum* subzone, and includes the cephalopod assemblages 1 to 3. Lithologically, this sequence is composed, in the north of the IT by bioclastic limestones with abundant burrows and algae laminations that upwards change to nodular biomicritic limestones. In the centre of the IT this sequence is constituted by flaggy to massive dolostones or limestones with less intense burrowing and algae lamination. As a whole, this first sequence corresponds to shallow marine platform deposits that experienced a slow and complex deepening (Carenas *et al*., 1989).

The boundary with the following sequence is marked by an interruption on the record of the Acanthoceratidae, till then continuous, together with the complete replacement of the identified genera and the appearance of the Vascoceratidae. Lithologically, this boundary corresponds to a net surface with a marked lithological change caused by a fast eustatic fall (Carenas *et al*., 1989).

5.2. Sequence B

It seems to coincide with the 3rd order depositional sequence UZA-2.5 of Haq *et al*. (1988) and with the sequences DC-6a and DC-6b of Floquet (1998), UC-



Substages	Depositional Sequences								
	Global	Iberian Trough, Spain				Western Portuguese Platform, Portugal		This work	
	Haq *et al.* (1988)	North-Castilian Sector Floquet (1998)	North-Castilian Sector Gräfe (1999)	Central Sector Alonso *et al.* (1993)	Central Sector Segura *et al.* (1999)	Callapez (1998)		Major	Minor
Lower Turonian	UZA-2.5	DC-6b	UC-6/7	DS-6 ↑	S-4	▨	▨	B	B 2
						L/(O)	(M/O)		
							L		
		DC-6a	UC-5/6			K	K		B 1
						▨ ?	▨		
Upper Cenomanian							J		
						B/J	E/I		
	UZA-2.4	DC-5	UC-4/5	DS-5	S-3	▨	▨	A	
						B/J ↓	C/D		
							B ↓		

Fig. 5.- Depositional sequences identified in the Iberian Trough and the Western Portuguese Carbonate Platform. The oblique lines indicate interval without record, and the arrows represent that the sequence continues.

Fig. 5.- Secuencias deposicionales identificadas en el Surco Ibérico y la Plataforma Carbonatada Occidental Portuguesa. Las líneas oblicuas indican intervalo sin registro, y las flechas representan que la secuencia continúa.

5/6 and UC-6/7 of Gräfe (1999), DS-6 of Alonso *et al*. (1993), in its lower and middle interval, and of S-4 of Segura *et al*. (1999). Its record, notably more expanded and rich than that of sequence A, ranges from the base of the *Vascoceras gamai* subzone to the top of the lower Turonian, and includes the cephalopod assemblages 4 to 9. Lithologically, this sequence is composed by biomicritic limestones that upwards change quickly to marls and, near the top, to chalky sandstones (notably dolomitized in the centre of the IT). It corresponds to an extraordinarily extensive sequence of open marine ramp, finally affected by a fast eustatic fall that generates a very prograding shallow marine platform (Segura *et al*., 1993).

This sequence can be divided in two others of lower order that can be related to the sequences DC-6a of Floquet (1998) and UC-5/6 of Gräfe (1999), and DC-6b of Floquet (1998) and UC-6/7 of Gräfe (1999), respectively. The first one, B_1, ranges from the base of the *Vascoceras gamai* subzone to the top of the *Spathites* (*Ingridella*) *malladae* subzone and includes the assemblages 4 to 6. In its upper limit another marked faunal change takes place, though of minor magnitude. The second one, B_2, ranges from the base of the *Choffaticeras* (*Leoniceras*) *luciae* subzone to the top of the lower Turonian, and includes the assemblages 7 to 9. In detail, lithologically, these two lower order sequences correspond to two prograding lithosomes separated by nodular limestones or marls (Floquet, 1991).

6. Discussion and conclusions

The above indicated facts suggest that assemblage 1 began after the disappearance of the cephalopods that dominated the IT during the latest middle Cenomanian, mainly *Acanthoceras*, caused by a marked worldwide marine regression. Seemingly, it coincided with a period in which, as consequence of a widespread and moderate eustatic ascent, the first ammonites typical of the earliest late Cenomanian, belonging to *Eucalycoceras* and *Calycoceras* and proceeding from the Protoatlantic, arrived to the Iberian Subplate and occupied some of the vacant ecologic niches.

Assemblage 2 seems to correspond to a faunal response to a marked and fast rise of the relative sea-level. This transgression both in the IT and WPCP made possible the permanency of *Calycoceras*, the appearance of new groups, such as *Lotzeites* and *Euomphaloceras*, and the record of several taxa of relatively deep waters in shallow platform sediments. Seemingly, the relative sea-level rise was kept the necessary time so that *Neolobites* could be

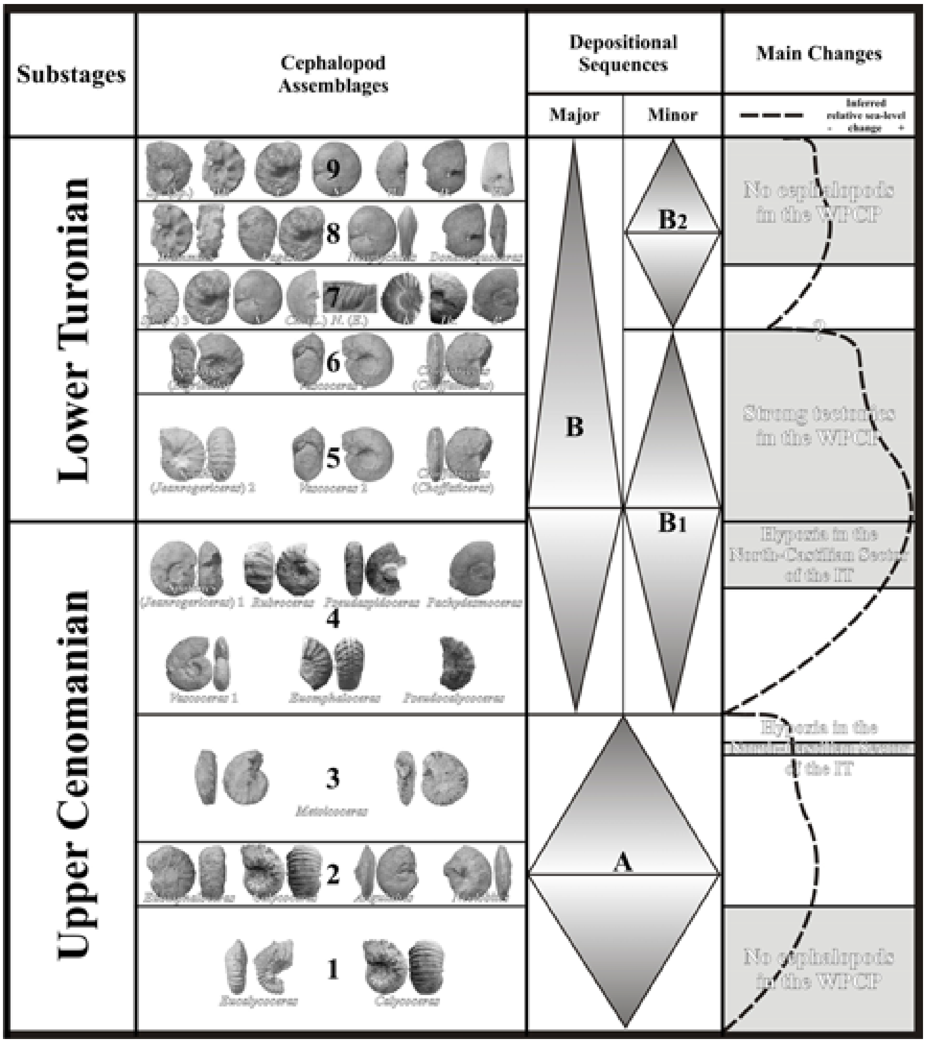


Fig. 6.- Main changes in the Iberian Trough and the Western Portuguese Carbonate Platform, inferred from the cephalopod assemblages and the depositional sequences (with graphic representations of the most important cephalopod groups and depositional cycles). *Sp*. (*J*.) 3 is *Spathites* (*Jeanrogericeras*) 3, *F*. is *Fagesia*, *N*. is *Neoptychites*, *Ch*. (*L*.) is *Choffaticeras* (*Leoniceras*), *N*. (*E*.) is *Nostoceras* (*Eubostrychoceras*), *K*. is *Kamerunoceras*, *Th*. is *Thomasites*, *P*. is *Pachydesmoceras*, *Sp*. (*Sp*.) is *Spathites* (*Spathites*), *M*. is *Mammites*, *W*. is *Wrightoceras*, *D*. is *Donenriquoceras*, and *H*. is *Hoplitoides*.

Fig. 6.- Principales cambios en el Surco Ibérico y la Plataforma Carbonatada Occidental Portuguesa deducidos de las asociaciones de cefalópodos y las secuencias deposicionales (con representaciones gráficas de los grupos de cefalópodos y ciclos deposicionales más importantes). *Sp*. (*J*.) 3 es *Spathites* (*Jeanrogericeras*) 3, *F*. es *Fagesia*, *N*. es *Neoptychites*, *Ch*. (*L*.) es *Choffaticeras* (*Leoniceras*), *N*. (*E*.) es *Nostoceras* (*Eubostrychoceras*), *K*. es *Kamerunoceras*, *Th*. es *Thomasites*, *P*. es *Pachydesmoceras*, *Sp*. (*Sp*.) es *Spathites* (*Spathites*), *M*. es *Mammites*, *W*. es *Wrightoceras*, *D*. es *Donenriquoceras*, y *H*. es *Hoplitoides*.

adapted to shallower environments, but not so that the representatives of other genera evolved to specialized forms of inner platform. The important taxonomic replacement observed among assemblages 2 and 3 could be related to the beginning of a drop on relative sea-level that favoured the disappearance of many of the cephalopods of the Iberian Subplate.

The interpretation of the assemblage 3 is extremely difficult, as it has numerous and complex indicators. In general, it could correspond to a fall on the relative sea-level (no known record in the WPCP and disappearance of *Angulithes* and *Neolobites*). Nevertheless, this change should be very moderate (establishment of *Metoicoceras* in the IT) and, even, could experience punctual ascending pulses, possibly related to the first and punctual phase of the OAE2 (*sensu* Barroso-Barcenilla *et al*., 2011). According to Meister *et al*. (1992), the practically exclusive presence of a species of cephalopod that shows a wide morphologic variability in a biostratigraphic interval is usually caused by the existence of a highly unstable environment in which the occupation of several ecological niches by a unique taxon was produced. Therefore, this seemingly unstable environment could be the cause of the presence in this assemblage of a single group (one genus: *Metoicoceras*) with certain morphologic variability (two species: *M. mosbyense* and *M. geslinianum*). Among assemblages 3 and 4, a whole replacement of the genera can be inferred. This change could be caused by a significant fall of the relative sea-level that deeply affected the sedimentary processes and the marine palaeobiotas of the Iberian Subplate. However, it does not seem rejectable that the same change was also influenced by the above indicated hypoxic event.

Assemblage 4 took place during the initial and intermediate stages of the great eustatic rise associated with the second and main phase of the OAE2 (*sensu* Barroso-Barcenilla *et al*., in press.) of the Cenomanian-Turonian Transition. Firstly and coinciding with the beginning of the relative sea-level rise, the fast widespread of the Vascoceratidae, specifically of *V. gamai* (one of its earliest members), happened. Secondly, these earliest *Vascoceras* diversified, giving place to some species almost exclusive of the Iberian Subplate, such as *V. barcoicense*, and even seemingly endemic, such as *V. charoni*, and the Acanthoceratidae returned to the region, by means of the earliest *S.* (*J.*) *subconciliatus*. Simultaneously, the WPCP experienced a notable arrival of American taxa, such as *Rubroceras*.

Nevertheless, this expansive process was interrupted by the effect of the second and main phase of the OAE2 that, with diverse intensity, concerned all the oceans of the planet. These new and unfavourable conditions of the epicontinental waters of the Iberian Subplate, although they should not have been very marked, since they did not cause the disappearance of the inoceramids in the Outer Navarro-Cantabrian Platform and the North-Castilian Sector, were responsible for the disappearance of all previous cephalopod taxa present up to this moment in the Iberian Subplate, except for *S.* (*J.*) *subconciliatus*. In fact, the practically exclusive presence of a species of cephalopod with a wide morphologic variability in a biostratigraphic interval (*S.* (*J.*) *subconciliatus* in this part of the homonymous zone) can be observed again and, as indicated by Meister *et al*. (1992), also seems to be caused by the existence of a highly unstable environment. This species, after overcoming the most intense phase of this palaeoceanographic crisis, occupied several of the vacant ecological niches, diversifying notably its morphology, especially in the IT. Likewise, the fact that the hypoxia affected more moderately the shallow than the deep marine environments allowed the subsistence of the Vascoceratidae in the IT and WPCP by means of *V. durandi* and *V. gamai*, among others.

Later, when the second and main phase of the OAE2 reduced its intensity, the adaptative process of *S.* (*J.*) *subconciliatus* continued, giving place to the varieties described by Wiedmann (1960, 1964) and to the endemic *S.* (*J.*) *robustus* in the IT. Finally, when the normal marine conditions came again and the high relative sea-level was reached, an important recovery of the Vascoceratidae began, being especially abundant *V. durandi*, and a significant arrival or return to the Iberian Subplate of exotic ammonoids of diverse origins, such as *V. cauvini*, *F. catinus* and *P.* (*A.*) sp. *P.* (*P.*) sp. and *P. denisonianum*, took place.

The transition between assemblages 4 and 5 is gradual and, seemingly, caused by progressive processes of adaptation to the favourable palaeoceanographic conditions and the arrival to the region of new taxa. This is valid for all the IT, but not for the WPCP where this was an interval of increased tectonic and diapiric activity, with uplift of the present onshore sectors of the Western Iberian Margin and subaerial exposure of the upper Cenomanian levels. These structural readjustments have been interpreted as the result of rotational movements within the subplate, but they could also be related to the tilting of the overall Iberian Ranges to the east or southeastwards. As a consequence of that and despite the contemporaneous sea-level highstand, there is no known record of marine carbonates on the WPCP below the middle part of lower Turonian.

Assemblage 5 corresponds to the beginning of the early Turonian, with a maximum relative sea-level and very favourable marine conditions that allowed the occupation of a great variety of ecological niches, the faunal exchange and the appearance of new taxa. Among others, the first Pseudotissotiidae arrived to the IT, who seemingly acceded to this region directly from the Tethys. Likewise, the arising of specialized morphologies proper of restricted ecologic niches, such as *S.* (*J.*) *saenzi* and *S.* (*J.*) *postsaenzi*, continued in the Acanthoceratidae, whereas the appearance of forms progressively more adapted to the epicontinental shallow environments persisted in the Vascoceratidae. In the development of the latter family the wide morphologic variability of *V. durandi* stood out. This seems to be an adaptative process to gradually more diverse ecological niches, similar to that followed by *S.* (*J.*) *subconciliatus* during the latest Cenomanian, with the subsequent appearance of successively more specialized forms, such as *V. amieirense* and *V. harttii*. As in the previous case, there are not strong differences between the taxonomic composition of assemblages 5 and 6, for what the transition between both was possibly produced as consequence of gradual evolutionary changes of adaptation to small modifications in the environmental conditions.

Assemblage 6 could be caused by a small fall of the relative sea-level. The same change would be influenced not only by a eustatic change but also by sedimentary accommodation and infill of the basin, which produced certain confinement of some areas of the IT, allowing the appearance of several nearly endemic taxa, among them *S.* (*I.*) *malladae* and *S.* (*J.*) *obliquus*. As consequence of the development of the long term evolutionary process followed by *Vascoceras* to give place to forms that are increasingly adapted to the shallow platform environments, specialized cadicones arose, such as *V. kossmati*. Likewise, *Wrightoceras* arrived to the IT by the first time. Except for *S.* (*J.*) *reveliereanus* (a widespread acanthoceratid with relatively long range), none of the species of the assemblage 6 have been identified in the assemblage 7. This fact seems to indicate that the ending of the assemblage 6 was probably produced by a sudden environmental change in the region. Possibly, a rapid and marked fall of the relative sea-level took place, which motivated the disappearance (in some cases temporary but in others definitive) of all shallow water taxa, such as *S.* (*Ingridella*) and *Vascoceras*.

Assemblage 7 seems to correspond to the faunal recovery that took place after the strong fall of the relative sea-level that led to the disappearance of nearly all marine environments of the Iberian Subplate for a time. In fact, a moderate rise of the relative sea-level made possible the arrival of some ammonites of pelagic spaces or higher bathymetries to this region. Among the species identified, seemingly *S.* (*J.*) *reveliereanus* could survive in relatively deep waters and, thus, overcome the absence of shallow environments. Supposedly, *Ch.* (*L.*) *luciae* and *Ch.* (*L.*) *barjonai* could not adapt to the IT, although they acceded often to the region (numerous records with no or minimum signs of taphonomic resedimentation or reelaboration in the Central Sector). In fact, the incursions of big predator oxycones, such as those of *Choffaticeras* (*Leniceras*), to very shallow and coastal waters already have been reported by Hewitt and Westermann (1989) and Kauffman (1990). *N.* (*E.*) sp. could install in the Outer Navarro-Cantabrian Platform and the North-Castilian Sector. In the WPCP this is the single lowest Turonian assemblage recorded with diverse and abundant faunas, clearly associated with a transgressive event related to the eustatic relative sea-level rising, but limited to certain parts of the basin.

Assemblage 8 seemingly took place during the advance of the relative sea-level rising that controlled the previous assemblage. The progress of the rising of the relative sea-level favoured the arrival of new taxa to the IT, principally from the Protoatlantic (*Mammites*: Wiedmann, 1975b; *Fagesia*: Kennedy and Cobban, 1976). Some of them could adapt to this region (again with vacant shallow epicontinental environments), and even gave place to ammonites practically exclusive of the IT (*Donenriquoceras*: Wright, 1996; Barroso-Barcenilla and Goy, 2007). Nevertheless, the relative sea-level must be lower than that reached during the span of assemblage 5, since it does not seem that the region had a direct connection with the Tethys (scarce number of cephalopods from this sea). Nearly all the groups identified in assemblage 8 can be recognized in assemblage 9. This fact suggests that any significant palaeoecological changes should have been produced during the transition between them.

Assemblage 9 seemingly was related to the stabilization of the favourable conditions on the IT. During its development, possibly a slight fall of the relative sea-level was produced, by eustatism or even by sedimentary fill of the basin, causing certain isolation in some areas of the region and the consequent appearance or recovering of several nearly endemic species. Nevertheless, the fall of the relative sea-level should be very moderated, since the marine epicontinental environments did not disappear, allowing the permanency, the appearance and the development of some cephalopods of these spaces. The Acanthoceratidae experienced a new diversification, which it made possible for *Spathites* to be represented by three subgenera, whereas *Fagesia* continued the adaptative process initiated time before. *Wrightoceras*, after coming from other basins of the Tethys, returned to the IT (in the absence of evidence of a direct connection with the Tethys, possibly around the Iberian Subplate), region that also was reached by the earliest Coilopoceratidae. Many of the species from the assemblage 9 disappear on the top of the lower Turonian where they are replaced by middle Turonian taxa, such as *Collignoniceras*, *Romaniceras* and *Coilopoceras*. This notable and global taxonomic replacement (very useful to establish the lower-middle Turonian boundary: Bengtson, 1996) could be caused by a marked fall on the relative sea-level that forced the extinction of numerous cephalopods in the IT.

Considering the changes produced during the development of the depositional sequences and their assemblages, some differences and several similarities between them can be established, which allow us to infer certain guidelines on the dynamics of the sequences. Among the differences, it stands out that the taxonomic diversity, and the abundance and variety of endemics are much lower in sequence A than in sequence B. This circumstance can be explained by the minor duration of the former sequence and the lower sea-level reached. Analyzing the palaeogeographic distribution of the exotics, it can be verified that the majority of those integrated in the sequences A and B_2 are mainly characteristic of the relatively cold and deep Protoatlantic, whereas the majority of those included in the sequence B_1 are fundamentally typical of the comparatively warmer and shallower Tethys. This fact can reflect a change in the influence received, which begins being principally Protoatlantic (from the base of the upper Cenomanian to the top of the *Metoicoceras geslinianum* subzone), changes being mainly Tethyan (between the *Vascoceras gamai* and *Spathites* (*Ingridella*) *malladae* subzones), and finishes being eminently boreal (from the top of the *Choffaticeras* (*Leoniceras*) *luciae* subzone to, at least, the base of the middle Turonian).

Among the similarities, it is remarkable that, without considering the possible changes caused by the geochemical oceanic variations and the evolutionary dynamics of the implied taxa, in each of the three differentiated sequences, a recurrence of the same succession of biotic events followed by their respective cephalopods can be inferred. Initially, the arrival of cosmopolitan forms of pelagic or deep environments, later, the appearance of derivative species from the previous ones relatively adapted to the shallow environments and, finally, the increase of the proportion of endemic forms can be observed (Text-fig. 6).

Though this succession of events is more difficultly observed in the major sequence A than in the minor ones B_1 and B_2 (possibly as consequence of the record being notably worse in the first one), each one of these intervals seems to correspond to successive periods of low, rising, and high relative sea-level, in which phenomena occurred respectively, of extinction of cephalopods from shallow environments, survival of taxa from pelagic or deep waters, settling of new spaces, and adaptation to them. Several studies have been developed recently relating sea-level changes and cephalopod faunal turnovers in the Mesozoic (O´Dogherty *et al*., 2000; Sandoval *et al*., 2002; Yacobucci, 2008). Specifically, when the sea-level goes down and the epicontinental environments disappeared, most of the cephalopods of shallow waters become extinct and only those that possessed certain aptitude to survive in open or deep oceanic environments overcame the crisis. During the sea-level rising, the cosmopolitan, pelagic or deep-water forms were the first ones to occupy the spaces available again as a consequence of the marine transgression in process, but soon they were replaced by others, derived from these cephalopods and better adapted to the shallow environments. Finally, specialized or nearly endemic taxa arose and dominated the region until, with the following fall of the sea-level, a new sequence began and a repetition of the described events occurred.

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APENDIX

Taxonomical list (generic, subgeneric, specific and subspecific ranks; E: Spain, P: Portugal)

Nautiloidea
Angulithes de Montfort, 1808
A. mermeti (Coquand, 1862) [E]
A. vascogoticus Wiedmann, 1960 [E]
Ammonoidea
Acanthoceratidae
Acanthoceras Neumayr, 1875
A. *rhotomagense* (Brongniart, 1822) [E]
Calycoceras Hyatt, 1900
C. (*Calycoceras*) Hyatt, 1900
C. (*C.*) *naviculare* (Mantell, 1822) [E, P]
C. (*C.*) sp. [E]
C. (*Proeucalycoceras*) Thomel, 1972
C. (*P.*) *guerangeri* (Spath, 1926a) [P]
C. (*P.*) sp. [E]
Eucalycoceras Spath, 1923a
E. pentagonum (Jukes-Browne, 1896) [P]
E. rowei (Spath, 1926a) [E]
Euomphaloceras Spath, 1923a
E. euomphalum (Sharpe, 1855) [E]
E. septemseriatus (Cragin, 1893) [P]
Kamerunoceras Reyment, 1954
K. douvillei (Pervinquière, 1907) [P]
K. ganuzai (Wiedmann, 1960) [E]
K. turoniense (d´Orbigny, 1850) [E]
Lotzeites Wiedmann, 1960
L. sp. [E]
Mammites Laube and Bruder, 1887
M. nodosoides (Schlüter, 1871) [E]
Metoicoceras Hyatt, 1903
M. geslinianum (d´Orbigny, 1850) [E]
M. mosbyense Cobban, 1953 [E]
Pseudaspidoceras Hyatt, 1903
P. pseudonodosoides Choffat, 1898 [P]
Pseudocalycoceras Thomel, 1969
P. sp. [P]
Romaniceras Spath, 1923a
R. (*Yubariceras*) Matsumoto *et al*., 1957
R. (*Y.*) *ornatissimum* (Stoliczka, 1864) [E]
Spathites Kummel and Decker, 1954
S. (*Ingridella*) Wiedmann, 1960
S. (*I.*) *depressus* (Wiedmann, 1960) [E]
S. (*I.*) *malladae* (Fallot, 1931) [E]
S. (*Jeanrogericeras*) Wiedmann, 1960
S. (*J.*) *combesi* (Sornay, 1951) [E]
S. (*J.*) *obliquus* (Karrenberg, 1935) [E]
S. (*J.*) *postsaenzi* (Wiedmann, 1960) [E]
S. (*J.*) *reveliereanus* (Courtiller, 1860) [E]
S. (*J.*) *robustus* (Wiedmann, 1960) [E]
S. (*J.*) *saenzi* (Wiedmann, 1960) [E]
S. (*J.*) *subconciliatus* (Choffat, 1898) [E, P]
S. (*J.*) *tavense* (Faraud, 1940) [E]
S. (*Spathites*) Kummel and Decker, 1954
S. (*S.*) *laevis* (Karrenberg, 1935) [E]
S. (*S.*) *sulcatus* (Wiedmann, 1960) [E]
Thomelites Wright and Kennedy *in* Juignet *et al*., 1973
T. hancocki Juignet and Kennedy, 1976 [P]

Vascoceratidae
- *Fagesia* Pervinquière, 1907
- *F. catinus* (Mantell, 1822) [E, P]
- *F. mortzestus* (Barroso-Barcenilla and Goy, 2009) [E]
- *F. pachydiscoides* Spath, 1925 [E]
- *F. rudra* (Stoliczka, 1865) [E]
- *F. superstes* (Kossmat, 1897) [E, P]
- *F. tevesthensis* (Peron, 1896) [E, P]
- *Neoptychites* Kossmat, 1895
- *N. cephalotus* (Courtiller, 1860) [E, P]
- *Rubroceras* Cobban *et al*., 1989
- *R.*cf. *alatum* Cobban *et al*., 1989 [P]
- *R.* sp. [P]
- *Vascoceras* Choffat, 1898
- *V. adonense* Choffat, 1898 [P]
- *V. amieirense* Choffat, 1898 [E]
- *V. barcoicense* Choffat, 1898 [E, P]
- *V. cauvini* Chudeau, 1909 [E]
- *V. charoni* (Barroso-Barcenilla and Goy, 2010) [E]
- *V. douvillei* Choffat, 1898 [P]
- *V. durandi* (Thomas and Peron, 1889) [E, P]
- *V. gamai* Choffat, 1898 [E, P]
- *V. harttii* (Hyatt, 1870) [E]
- *V. kossmati* Choffat, 1898 [E, P]
- *V. silvanense* Choffat, 1898 [P]
- *V.* sp. [P]

Pseudotissotiidae
- *Choffaticeras* (*Choffaticeras*) *pavillieri* (Pervinquière, 1907) [E]
- *Ch.* (*Ch.*) *quaasi* (Peron, 1904) [E]
- *Ch.* (*Ch.*) *segne* (Solger, 1903) [E]
- *Ch.* (*Ch.*) *sinaiticum* (Douvillé, 1928) [E]
- *Choffaticeras* (*Leoniceras*) Douvillé, 1912a
- *Ch.* (*L.*) *barjonai* (Choffat, 1898) [E, P]
- *Ch.* (*L.*) *luciae* (Pervinquière, 1907) [E]
- *Donenriquoceras* Wiedmann, 1960
- *D. forbesiceratiforme* Wiedmann, 1960 [E]
- *Pseudotissotia* Peron, 1897
- *P.* sp. [E]
- *Thomasites* Pervinquière, 1907
- *T. rollandi* (Thomas and Peron, 1889) [P]
- *Wrightoceras* Reyment, 1954a
- *W. llarenai* (Karrenberg, 1935) [E]
- *W. munieri* (Pervinquière, 1907) [E]
- *W. submunieri* Wiedmann, 1975b [E]

Other families
- *Coilopoceras* Hyatt, 1903
- *C.* sp. [E]
- *Hoplitoides* von Koenen, 1898
- *H. ingens* (von Koenen, 1897) [E]
- *Hypophylloceras* Salfeld, 1924
- *H.* (*Neophylloceras*) Shimizu, 1934
- *H.* (*N.*) sp. [E]
- *Parapuzosia* Nowak, 1913
- *P.* (*Austiniceras*) Spath, 1922a
- *P.* (*A.*) sp. [E]
- *P.* (*A.*) *intermedia orientalis* Matsumoto, 1954 [P]
- *Puzosia* Bayle, 1878
- *Puzosia* (*Puzosia*) sp. [P]
- *Pachydesmoceras* Spath, 1922a
- *P. denisonianum* (Stoliczka, 1865) [P]
- *P. linderi* (de Grossouvre, 1894) [E]
- *Neolobites* Fischer, 1882
- *N. bussoni* Collignon, 1965b [P]
- *N. vibrayeanus* (d´Orbigny, 1841) [E, P]
- *Nostoceras* Hyatt, 1894
- *N.* (*Eubostrychoceras*) Matsumoto, 1967
- *N.* (*E.*) sp. [E]

Gastropoda
- *Actaeonella caucasica* Zekelli, 1847 [P]

Bivalvia
- *Gyrostrea ouremensis* Choffat, 1898 [P]