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
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

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...

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 marls tones), 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 Lusitanian 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
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 re-sedimentation or re-elaboration (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 paleoecologic turnovers that happened in the studied basins, both with external origin or due to local tectonic and paleogeographical changes. Each of them has been interpreted considering the narrow relation that was established in the epicontinental platforms between the paleoecologic changes and the general paleontological 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* (Proeucaulycoceras) sp., *Calycoceras* (Calycoceras) sp. and, seemingly, *Calycoceras* (Calycoceras) navicularare, have been identified, all of them belonging to the Acanthoceratidae. In the WPCP its lower part corresponds to a stratigraphic interval with the bivalve *Gyrostrexa 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 vibrayeans* 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 vibrayeans* and *Calycoceras* (Calycoceras) navicularare, in both basins; *Lotzeites* sp. and *Euomphaloceras euomphalum*, in the IT; and *Neolobites bussoni*, *Calycoceras* (Proeucaulycoceras) 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 *Metiococeras mosbyense* and *Metiococeras geslinianum* subzones of the IT, where includes the co-occurrence of *Metiococeras*, and only owns the species *Metiococeras mosbyense* and *Metiococeras 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 Puente de Cuello Section, the materials corresponding to the *M. geslinianum* subzone registered the first and punctual of the two positive excursions of the δC13 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 septenceriatus* and the *Pseudaspidocearas 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 *Pseudaspidocearas*, 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 septenceriatus*, *Vascoceras adonense*, *Vascoceras silvanense*, *Vascoceras* sp., *Vascoceras dovillei*, *Vascoceras kossmati*, *Rubroceras* cf. *alatum*, *Rubroceras* sp., *Pseudaspidocearas 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-
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 (41) 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 (42) 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 δC13 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
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 spantan-goids 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 (Tama-jón: 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 *Pachydes-moceras* 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 Pseudotissotiiidae, with the species *Spathites* (Jeanrogericeras) *subconciliatus*, *Spathites* (Jeanrogericeras) *tavense*, *Spathites* (Jeanrogericeras) *saenzi*, *Spathites* (Jeanrogericeras) *postsaenzi*, *Vascoceras* *durandi*, *Vascoceras* amieirense, *Vascoceras* hartti, *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, phylo-
genetic relationships can be established between almost all the represented species (Acanthoceratidae: Barroso-Barcenilla, 2007; Vascoceratidae: Barroso-Barcenilla and Goy, 2009, 2010; Pseudotissotiiidae: 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 pseudotisso-
tiids (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) oblquus, Spathites (Jeanrogericeras) reveliereanus, Kamerunoceras ganuzai, Vascoceras amieirense, Vascoceras harti, Vascoceras kossmati, Choffaticeras (Choffaticeras) pavilli, Choffaticeras (Choffaticeras) sinaicum, Wrightoceras llarenai, Angulithes vascogoticus and, possibly, Choffaticeras (Choffaticeras) sege. 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 denisonium 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 Pseudrotissotiiidae, and of Nostoceras (Eubostrychoceras), in the Nostoceratidae, in the former region, and of Kamerunoceras, in the Acanthoceratidae, of Fagesia with Neopbychites, in the Vascoceratidae, of Choffaticeras (Leoniceras) with Thomasites, in the Pseudotissotiiidae, 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, Neopbychites cephalotus, Thomasites rollandi, Choffaticeras (Leoniceras) barjonai, Pachydesmoceras denisonium 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 Neopbychites, 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 Neopbychites, with the species Mammites nodosoides, Spathites (Jeanrogericeras) reveliereanus, Fagesia tevesthensis, Fagesia rudra, Fagesia mortezus, Fagesia superstes, Neopbychites cephalotus, Donenriquoceras forbesiiceratiforme and Pachydesmoceras linderi. In the WPCP it corresponds to a stratigraphic interval with gastropods of the species Actaeonella caucasia 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 Cobb, 1976), but those from relatively open and deep environments, such as Neopbychites (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 *Doneniiquoceras*, in the Pseudotissotidae, of *Hopliotoides*, in the Coilopeceratidae, and the upper part of *Fagesia* with *Neopytchites*, 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, *Neopytchites cephalotus*, *Wrightoceras* munieri, *Doneniiquoceras forbesiceraiforme* and *Hoplioides ingen*). 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 B1, and K/L and M/O with B2 (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 B1 and B2, 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 *Metoiococe-ras 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 biomericitic 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-
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

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<table>
<thead>
<tr>
<th>Substrates</th>
<th>Lower Turonian</th>
<th>Upper Cenomanian</th>
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<tbody>
<tr>
<td><strong>Depositional Sequences</strong></td>
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<tr>
<td>Global</td>
<td>Iberian Trough, Spain</td>
<td>Western Portuguese ramp, Portugal</td>
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<tr>
<td>Hag et al. (1988)</td>
<td>North-Cantabrian Sector Floquet (1998)</td>
<td>This work</td>
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<td>Central Sector Segura et al. (1999)</td>
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<td><strong>Subzones</strong></td>
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<td>UZA-2.5</td>
<td>DS-6</td>
<td>S-4</td>
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<td>DC-6b</td>
<td>UC-6/7</td>
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<td><strong>Subzones</strong></td>
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<td>B 1</td>
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<tr>
<td>UZA-2.4</td>
<td>DS-5</td>
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<td>DC-5</td>
<td>UC-4/5</td>
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<td>UC-6/7</td>
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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, B1, ranges from the base of the *Vascoceras gamai* subzone to the top of the *Spathamites (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, B2, 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).
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: *Metococeras*) with certain morphologic variability (two species: *M. mosyvense* 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.) subconcziliatus*. 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 epicontinental waters of the Iberian 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 adaptive process to gradually more diverse ecological niches, similar to that followed by *S. (J.) subconcziliatus* 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 evolu-

Later, when the second and main phase of the OAE2 reduced its intensity, the adaptive process of *S. (J.) subconcziliatus* 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. denisoni-um*, 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.
tionary 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 *Vasoceras* to give place to forms that are increasingly adapted to the shallow platform environments, specialized cadicones arose, such as *V. koss-matti*. 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 *Vasoceras*.

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 reellation 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-Barcennilla 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 *Collignonioceras*, *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 B₂ are mainly characteristic of the relatively cold and deep Protoatlantic, whereas the majority of those included in the sequence B₁ 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 *Metococeras geslinianum* subzone), changes being mainly Tethyan (between the *Vascoceras gamai* and *Spathites (Ingridella) mallaedae* 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 B₁ and B₂ (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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**References**


Section and Point for the base of the Turonian Stage of the Cretaceous, and for the base of the Middle Turonian Substage, with a revision of Inoceramidae (Bivalvia). *Acta Geologica Polonica*, 50: 295-334.


**APENDIX**

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

**Nautiloidea**

_Angulithec_ 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. (Proeuclrococeras)_ Thomel, 1972
_C. (P.) gueraangeri_ (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_ (Pervinquiére, 1907) [P]
_K. ganizai_ (Wiedmann, 1960) [E]
_K. turowiensis_ (d'Orbigny, 1850) [E]
_Latzeites_ Wiedmann, 1960
_L. sp._ [E]
_Mammites_ Laube and Bruder, 1887
_M. nodosoides_ (Schützer, 1871) [E]

**Metoicoceras_ Hyatt, 1903**
_M. gestlinianum_ (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 Deckers, 1954
_S. (Ingridella)_ Wiedmann, 1960
_S. (I.) depressus_ (Wiedmann, 1960) [E]
_S. (I.) mulladus_ (Fallot, 1931) [E]
_S. (Jeanrogericeras)_ Wiedmann, 1960
_S. (I.) combesi_ (Sornay, 1951) [E]
_S. (I.) obliquus_ (Karrenberg, 1935) [E]
_S. (J.) postsaenzi_ (Wiedmann, 1960) [E]
_S. (J.) revelleicanus_ (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 Deckers, 1954
_S. (S.) inaevis_ (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. douvilleti Choffat, 1898 [P]
V. durandi (Thomas and Peron, 1889) [E, P]
V. gamai Choffat, 1898 [E, P]
V. hartii (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]
Thomasiter Pervinquière, 1907
T. rollandi (Thomas and Peron, 1889) [P]
Wrightoceras Reymond, 1954a
W. ilarenai (Karrenberg, 1935) [E]
W. munieri (Pervinquière, 1907) [E]
W. submunieri Wiedmann, 1975 [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 Nowák, 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 Gossouvre, 1894) [E]
Neolobites Fischer, 1882
N. bussoni Collignon, 1965 [P]
N. vibrayeanus (d’Orbigny, 1841) [E, P]
Nostoceras Hyatt, 1894
N. (Eubostryhoceras) Matsumoto, 1967
N. (E.) sp. [E]
Gastropoda
Actaeonella caucasica Zekelli, 1847 [P]
Bivalvia
Gyrostrea ouremica Choffat, 1898 [P]