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Lower Jurassic brachiopods from the Ibero-Levantine Sector (Iberian Range): Faunal turnovers and critical bioevents

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Abstract

Brachiopod fauna from the peri-Iberian platform system is well-known in the Late Pliensbachian-Toarcian interval. However, the diversity dynamics and the stratigraphical distribution of this group in the Ibero-Levantine Sector of the Iberian Range require more accurate analysis due to the patchy distribution of the outcrops. The abovementioned timespan involved a period of changes in long-term environmental conditions which led to a severe extinction and critical turnovers on the brachiopod fauna (ETMEE). The Ibero-Levantine sector has notable palaeobiogeographical significance as it represents the south-easternmost outcrops of the Iberian Range connecting with the Betic Domain positioned in the South-Iberian Palaeomargin. In this region, the brachiopod fauna has been arranged into six assemblages, showing a discontinuous stratigraphic distribution since its diversity dynamics is markedly conditioned by the extinction phases linked to the ETMEE: Ass. 1, recorded in the Spinatum-lower Tenuicostatum chronozones; Ass. 2, mainly recorded in the Tenuicostatum chronozone; Ass. 3, typifying the lower Serpentinum chronozone; Ass. 4, documented in the Serpentinum-lowermost Bifrons chronozones; Ass. 5, recorded in the Bifrons-Variabilis chronozones, and Ass. 6, distinctive of the Pseudoradiosa-Aalensis chronozones.

The faunal succession shows strong affinities with the Euro-Boreal province, what rules out the transitional or even Mediterranean palaeogeographical affinity previously attributed to the southernmost part of this area. Amidst the main brachiopod-based bioevents must be considered the predominance of the genus *Lobothyris* in the pre-ETMEE assemblages, the conspicuous record of *Liospiriferina*? *undulata*, distinctive taxon of the north-African margin and, especially, the first record in the Iberian Peninsula of thecideid marker beds prior to the ETMEE. After the opportunistic strategy conducted by *Soaresirhynchia bouchardi* the distribution of the post-ETMEE brachiopod assemblages is markedly influenced by the depositional sequences, entailing premature turnovers and involving the earlier record of homeomorphic morphotypes of younger terebratulides and rhynchonellides.

Keywords: Brachiopods, Western Tethys, Early Jurassic, palaeobiogeography, mass extinction, faunal turnovers

Resumen

Las sucesiones de braquiópodos en el Pliensbachiense superior-Toarciense, ampliamente reconocidas en las plataformas marginales de Iberia, carece de un registro preciso en el sector Ibero-Levantino de la Cordillera Ibérica. Este intervalo engloba un periodo de cambios ambientales significativos, incluyendo un severo evento de extinción y reemplazamiento que condiciona notablemente la distribución de los braquiópodos (ETMEE). El sector Ibero-Levantino posee un especial interés paleobiogeográfico, representando el extremo sudoriental de la Cordillera Ibérica, en contacto con los afloramientos de directriz Bética del paleomargen sud-Ibérico. En esta región, se han definido seis asociaciones que muestran gran similitud con las del resto de áreas epicontinentales de la Cordillera Ibérica, si bien presentan unos bioeventos diferenciadores: As. 1, registrada en la cronozona Spinatum-parte baja de Tenuicostatum; As. 2, fundamentalmente reconocida en la cronozona Tenuicostatum; As. 3, característica de la cronozona Serpentinum (parte basal); As. 4, registrada en las cronozonas Serpentinum-parte inferior de Bifrons; As. 5, distintiva de las cronozonas Bifrons-Variabilis y As. 6, típica de las cronozonas Pseudoradiosa-Aalensis. Paleobiogeográficamente, no se registra (pre-ETMEE) ningún taxón distintivo de la provincia Mediterránea, al contrario que en las cuencas béticas contiguas, descartándose el carácter transicional e incluso "bético" que se confería a los afloramientos meridionales de esta región. Entre los bioeventos excepcionales cabe destacar el primer hallazgo de un nivel guía pre-ETMME de Thecideidos, no documentado hasta el momento en el resto de plataformas marginales de Iberia. También es diferenciador el bioevento pre-ETMEE de máxima diversidad y abundancia de *Liospiriferina*? *undulata*, taxón característico del margen nord-africano, así como una mayor persistencia del género *Lobothyris*. Tras el ETMEE, se aprecia la estrategia oportunista de *Soaresirhynchia bouchardi* y una prematura aparición de la As. 5 respecto al resto de la Cordillera Ibérica, confirmando la estrecha relación entre las sucesiones faunísticas y los continuos cambios de facies durante el Toarciense-Aaleniense.

Palabras clave: Braquiópodos, Tethys occidental, Jurásico Inferior, paleobiogeografía, extinción masiva, reemplazamiento faunístico

1. Introduction

Lower Jurassic brachiopods have been widely documented in the Iberian Range, especially in the Pliensbachian-Toarcian interval (Dubar, 1931; Goy and Robles, 1975; Comas-Rengifo and Goy, 1975; Goy *et al*., 1984; 1997; García Joral and Goy, 1984, 1994, 2000, 2004; García Joral *et al*., 1990, 2011; Comas-Rengifo *et al*., 1998, 2006, among others). Whereas an extensive research has been carried out on the brachiopod faunas of the northern and innermost areas of the basin (Castilian and Aragonese branches), the Ibero-Levantine Sector (I-LS hereinafter) of the Iberian Range remains insufficiently studied, probably due to the patchy distribution of the outcrops, particularly in the southern part of this region (Gómez, 1979).

The Ibero-Levantine region is located in a strategic palaeobiogeographical situation, representing the south-easternmost outcrops of the Iberian Range connecting with the Betic Domain positioned in the South-Iberian Palaeomargin. The epicontinental carbonate environments in this region are prolific in macroinvertebrates (mainly bivalves, ammonites and brachiopods). The detailed analysis of brachiopod assemblages for the first time in this area and the calibration of its distribution with the exhaustively controlled biochronological ammonite data at zone (even biohorizon) level in the Iberian Range (Goy, 1974; Goy *et al*., 1988; Goy and Martínez, 1990) contribute to a better understanding the palaeobiogeographic evolution (at a regional and global scale) of the peri-Iberian platform system established during the Early Jurassic.

The Lower Jurassic brachiopod successions in the I-LS are recorded in the uppermost Pliensbachian-Upper Toarcian interval, comprising a period of changes in long-term environmental conditions (e.g. Little and Benton, 1995; Wignall *et al.,* 2005; cf. Wignall and Bond, 2008; Caswell et al., 2009) which led to a main biotic crisis event (Early Toarcian Mass Extinction Event, ETMEE) entailing a conspicuous extinction and severe turnover of the brachiopod fauna (e.g. Little and Benton, 1995; Vörös, 2002; García Joral *et al*., 2011; Baeza-Carratalá *et al*., 2015; Vörös *et al*., 2016). In the I-LS outcrops, the dynamics of the brachiopod assemblages is markedly conditioned by this event, showing a high diversity in the assemblages but with a discontinuous stratigraphic distribution related with the extinction phases linked to the ETMEE. Thus, the analysis of the assemblages, diversity turnovers and the main brachiopod-based bioevents prior to the ETMEE and their posterior recovery in this area, improves the knowledge of the ecological effects of this event in the peri-Iberian basins, which include one of the most conspicuous brachiopod records around the ETMEE in the westernmost Tethyan Ocean.

Previous significant contributions to the knowledge of the Lower Jurassic Ibero-Levantine brachiopods were scarce, e.g. by Bizon *et al*. (1966) and Champetier (1971, 1972), who reported brachiopod occurrences restricted to the Spinatum Zone and the Pliensbachian-Toarcian transition. The subsequent comprehensive stratigraphical work of Gómez (1979) revealed, in the Sot de Chera locality (besides of *Rhynchonella* cf. *dumbletonensis, Spiriferina rostrata* and *Lobothyris arcta*, prior to the ETMEE), the first evidence of post-ETMEE brachiopod fauna, reporting *S. bouchardi* together with several typical Middle-Upper Toarcian taxa. This work also included several outcrops northwards containing brachiopods with predominance of *H. meridionalis* and *S. bouchardi.*

The present work reveals the variations in the diversity and taxonomical composition of the brachiopod assemblages prior to- and post-ETMEE, up to their total recovery in the Middle-Late Toarcian times. This analysis suggests several brachiopod-based bioevents, such as the conspicuous occurrence of micromorphic, mainly thecideoid representatives, which typify a pre-ETMME marker bed in the I-LS. This bioevent is recorded for the first time in the Iberian Range as well as in the entire peri-Iberian platforms system.

Analyzing the distribution and calibrating the Ibero-Levantine brachiopod assemblages enable their use, not only for the palaeogeographical reconstructions, but also for biostratigraphical purposes as being achieved in all other peri-Iberian platforms (Goy *et al*., 1984; García Joral *et al*., 1990, 2011; Fernández-López *et al*., 1998; García Joral and Goy, 2000; 2009, 2010; Baeza-Carratalá and García Joral, 2012; Baeza-Carratalá, 2013; Comas-Rengifo *et al*., 2015; Baeza-Carratalá *et al*., 2016).

Finally, this work also improves the knowledge of the Middle-Late Toarcian assemblages of the Iberian Range, which have notable palaeobiogeographic implications due to their potential for dispersion throughout the peri-Laurasian epicontinental platforms (Andrade, 2006; Baeza-Carratalá and Sepehriannasab, 2014; Andrade *et al*., 2016).

2. Geological and stratigraphical setting

Several Jurassic localities have been prospected in the I-LS of the Iberian Range. The outcrops are often patchily distributed and discontinuous but some localities allow bed-by-bed sampling. Three of these localities (Racó de Joana, Benifairó-

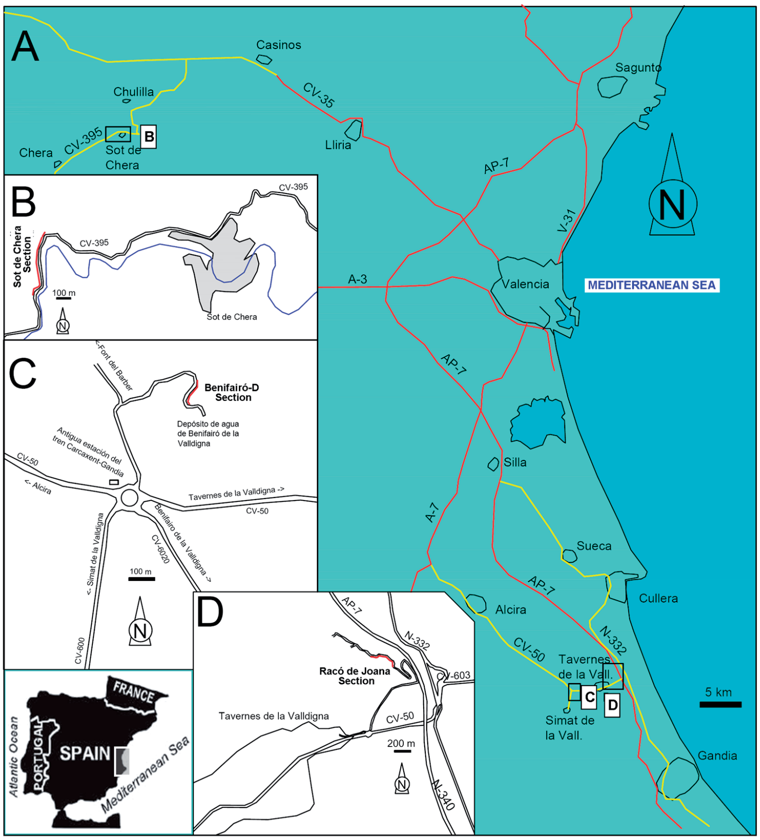


Fig. 1.- A. Geographical situation of the sampled localities in the Ibero-Levantine sector of the Iberian Range (Valencia province, Spain). Stratigraphical sections are detailed in B: Sot de Chera section, C: Benifairó-D section, and D: Racó de Joana section.

D, and Sot de Chera) located in the Valencia province (East Spain), have been selected being the most appropriate to establish brachiopod successions in this sector (Fig. 1).

The Ibero-Levantine sector (*sensu* Gómez, 1979) comprises the southernmost Jurassic outcrops of the Iberian Range, close to the Prebetic outcrops (Fig. 2). Northwards, this sector gives way to the Castilian branch, bordering to the Northwest with the Aragonese branch of the Iberian Range (Fig. 2). All of them together with the South Iberian palaeomargin (mainly represented by the Betic Domain), the Lusitanian, Asturias and the Basque-Cantabrian basins, constituted a system of platforms distributed around the Iberian Subplate in the Early Jurassic (Gómez and Goy, 2005).

The lithostratigraphic framework of the Lower Jurassic outcrops is quite similar in all regions of the Iberian Range (Gómez *et al*., 2003). The Upper Pliensbachian-Toarcian sediments are represented, from bottom to top, by the Barahona Fm., Turmiel Fm., and Casinos Fm. (Fig. 2).

In the studied outcrops, the Barahona Fm. is mainly composed by grayish to yellowish-red bioclastic grainstone-packstone beds with abundant bivalves (mainly ostreids) and crinoids; individual beds are less than 1 m-thick. The top of this unit is marked by a 0.5 m-thick, orange-color, condensation level bounded by two hardground levels (Goy *et al.,* 1976). It is rich in skeletal remains, mainly corresponding to bivalves, gastropods, brachiopods, and scarce echinoids, and is especially developed in the Sot de Chera and Racó de Joana sections (Fig. 3). These deposits are referred as "*Barahona hardground*" (cf. Goy *et al*., 1976).

From the Pliensbachian-Toarcian transition onwards, the facies dominating all the outcrops are an alternation of grey and yellowish marls and mudstone beds of the Turmiel Fm. (Figs. 4, 5), which are arranged into deepening- and shallowing-upwards sequences (Gómez and Goy, 2000). At the bottom of this unit, a discontinuous shell-bed consisting of abundant brachiopod specimens can be found in Racó de Joana and Benifairó-D sections.

Finally, the Casinos Fm. characterizes the Middle-Upper Toarcian deposits with a sedimentation related with the onset of progradation of a marginal carbonate platform (Gómez and Goy, 2005). This unit is mainly composed of grayish mudstone to wackestone beds commonly with marly levels interspersed. They are well-bedded strata arranged in thin (10 to 20 cm-thick) layers. Some set-layers of this unit show characteristic kidney-shaped bedding surfaces and, in the upper part of the Benifairó-D section, the calcareous sedimentation becomes thicker and more massive (Figs. 4, 5).

The record of the bottom of the Casinos Fm., and hence the onset of the mainly carbonate sedimentation, has proved to be relevant for the distribution of the brachiopod fauna as discussed later. In the Early-Middle Jurassic, the Iberian Range suffered a strong differentiation of the basin. As a consequence, evident variation of facies, thickness and development of disconformities occurred (cf. Gómez and Goy, 1979, 1981; García Joral *et al*., 1990). Thus, the transition from the marly Turmiel Fm. to the calcareous Casinos Fm. can be regarded as diachronic (Gómez, 1979), since it took place earlier in the I-LS (Bifrons-Variabilis zones) than in the

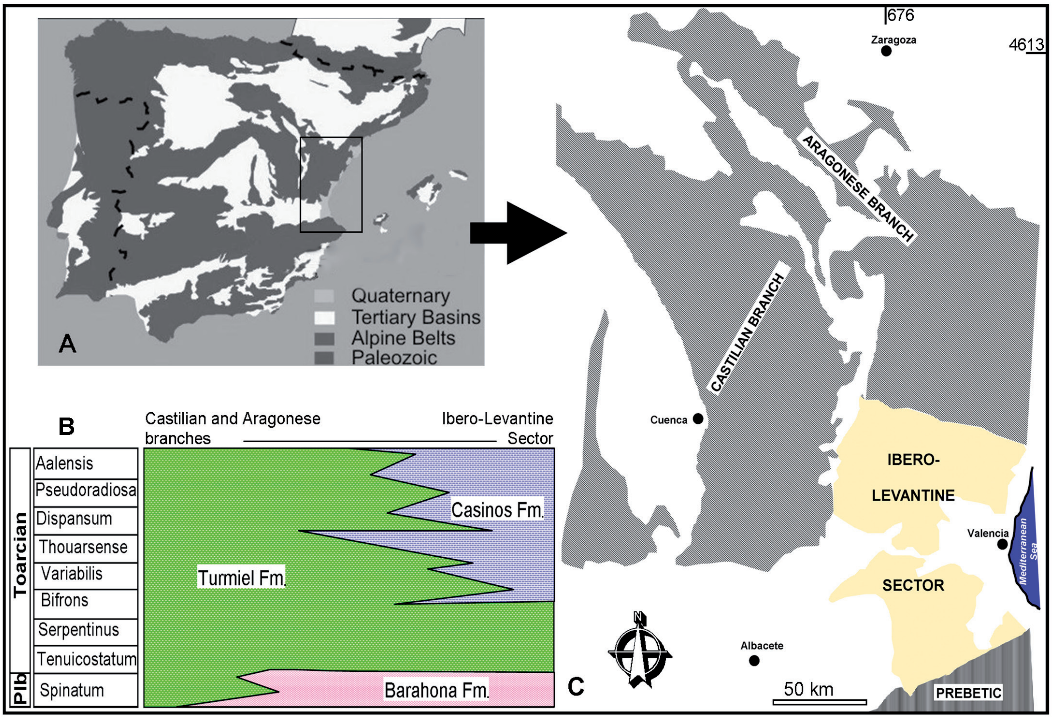


Fig. 2.- A. Geological setting of the Ibero-Levantine sector within the major geological domains of the Iberian Peninsula. B. Simplified sketch showing the lithostratigraphical framework of the Lower Jurassic formations in the studied area (slightly modified after Gómez and Goy, 2005). C. Regional geological sketch of the Ibero-Levantine outcrops in relationship to neighbouring areas.

remaining areas of the Iberian Range (Pseudoradiosa Zone-Lower Bajocian), noticeably conditioning the distribution of the brachiopod successions (García Joral *et al*., 1990).

3. Materials and methods

Brachiopod-bearing deposits were analysed and sampled bed by bed. The samplings yielded 1692 specimens in three stratigraphic sections which contain the most complete and fossil-rich successions: Sot de Chera, Benifairó-D, and Racó de Joana (Fig. 1). Sot de Chera section partially corresponds to the section with the same denomination previously studied by Gómez (1979). Benifairó-D and Racó de Joana sections were previously sampled respectively as “Fuente del Barbero” and “Recó Juana” (sic) sections (Bizón *et al*., 1966; Champetier, 1971, 1972).

Generic assignments follow the published diagnoses mainly in the *Treatise* (Kaesler and Selden, 1997-2007). The internal structure of the thecideid fauna was directly studied under the stereo microscope on both disarticulated pedicle and brachial valves. All specimens were coated with magnesium oxide before photographing. High-resolution images were taken for the micromorphic thecideid fauna. All specimens are deposited at Departamento de Ciencias de la Tierra y del Medio Ambiente (University of Alicante, Spain).

The ammonite zonal/subzonal scheme follows the standard proposed by Dommergues *et al.* (1997), Elmi *et al.* (1997) and Page (2003) for the Jurassic of the NW-European Domain.

4. Compositional analysis and assemblages distribution

Brachiopod fauna from the I-LS can be arranged into six assemblages. These assemblages, albeit showing some distinguishing attributes, reveal a great similarity with those recorded in the remaining epicontinental platforms from the Iberian Range. Thus, they have been determined following the same palaeobiogeographic and chronostratigraphic criteria established in such areas (e.g. García Joral and Goy, 2000; García Joral *et al.,* 2011):

Assemblage 1 (Figs. 4-6): [=Ass. 1 (*partim* García Joral and Goy, 2000; *in toto* García Joral *et al*., 2011)]. It consists of *Lobothyris* gr. *punctata* (Sowerby, 1813), *L. subpunctata* (Davidson, 1851), *Aulacothyris resupinata* (Sowerby, 1816), and *Liospiriferina nicklesi* (Corroy, 1927). It is recorded at the top of the Barahona Fm., or equivalent levels and in the overlying lower beds of the Turmiel Fm. It occurs in the Spinatum-lowermost Tenuicostatum chronozones.

Assemblage 2 (Figs. 4-6): [=Ass. 1 (*partim* García Joral and Goy, 2000); =Ass. 2 (García Joral *et al*., 2011)]. It is represented by *Quadratirhynchia attenuata* (Dubar, 1931), *Liospiriferina*? *undulata* (Seguenza, 1883), *Liospiriferina* sp. ind., *Lobothyris arcta* (Dubar, 1931), and a copious thecideid fauna (mainly arranged as *Eudesella* specimens), as index taxa. This assemblage also includes regularly associated *Aulacothyris iberica* (Dubar, 1931), *Dispiriferina*? *oxyptera* (Buvignier, 1843) and *Liospiriferina* cf. *terebratuloides* (Seguenza, 1883) as representative fauna. It is recorded in the Turmiel Fm., occurring in the Tenuicostatum Chronozone, though several taxa can co-occur with the Assemblage 1 in the uppermost Spinatum Zone.

Assemblage 3 (Figs. 4, 6): [=Ass. 2 (García Joral and Goy, 2000); =Ass. 3 (García Joral *et al*., 2011)]. It appears as monospecific concentrations of *Soaresirhynchia bouchardi* (Davidson, 1852) but the last records of this taxon can be found together with several Rhynchonellids belonging to the subsequent assemblage (Ass. 4). It is recorded in the Turmiel Fm. occurring in the lower part of the Serpentinum Chronozone (usually recorded in the Elegantulum Subzone).

Assemblage 4 (Figs. 4, 5, 7): [=Ass. 3 (García Joral and Goy, 2000); =Ass. 4 (García Joral *et al*., 2011)]. It is made up by *Homoeorhynchia meridionalis* (Deslongchamps, 1863), *H. batalleri* (Dubar, 1931), *Pseudogibbirhynchia* ex gr. *jurensis* (Quenstedt, 1858), *Telothyris jauberti* (Deslongchamps, 1863), *T. pyrenaica* (Dubar, 1931), and *Lobothyris*? *hispanica* (Dubar, 1931). They typify the so-called “Spanish Bioprovince” of brachiopods (García Joral and Goy, 1984; 2000; García Joral *et al*., 2011). It is recorded in the Turmiel Fm., occurring in the Serpentinum- (lowermost) Bifrons chronozones.

Assemblage 5 (Figs. 4, 5, 7): [=Ass. 4 + Ass. 5 (García Joral and Goy, 2000)]. It includes *Homoeorhynchia*? *marini* (Rousselle, 1975), *H. pusilla* García Joral and Goy, 2010, *Choffatirhynchia* aff. *turolensis* García Joral and Goy, 2004, *Rhynchonelloidea* aff. *goyi* García Joral, 1983, *Pseudogibbirhynchia* ex gr. *jurensis s.l.* (Quenstedt, 1858), a closely related (but different) species with that aforementioned in the Ass. 4, *Telothyris* sp. 1, *Stroudithyris* aff. *infraoolithica* (Deslongchamps, 1871), *Stroudithyris* sp., and *Neozeilleria* cf. *lycetti* (Davidson, 1851) as representative taxa. It is recorded in the Casinos Fm., occurring in the Bifrons-Variabilis chronozones.

Assemblage 6 (Fig. 5): [=Ass. 6 (García Joral and Goy, 2000)]. This assemblage is only represented in this sector by the occurrence of scarce and very fragmentary specimens of *Rhynchonelloidea goyi* García Joral, 1983, and large-sized unspecified terebratulids. It is recorded in the Casinos Fm., occurring in the Pseudoradiosa-Aalensis chronozones.

5. Discussion. Critical bioevents and faunal turnovers

Brachiopod faunal successions from the I-LS are recorded in the uppermost Pliensbachian-Toarcian interval. This time-span comprised a period of long-term environmental changes entailing a severe biotic crisis for the Mesozoic epibenthic biota, giving rise to a conspicuous extinction event (ETMEE) and/or severe turnovers on the brachiopod fauna (e.g. Little and Benton, 1995; Vörös, 2002; García-Joral *et al*., 2011; Baeza-Carratalá *et al*., 2015; Ruban and Vörös, 2015). In the

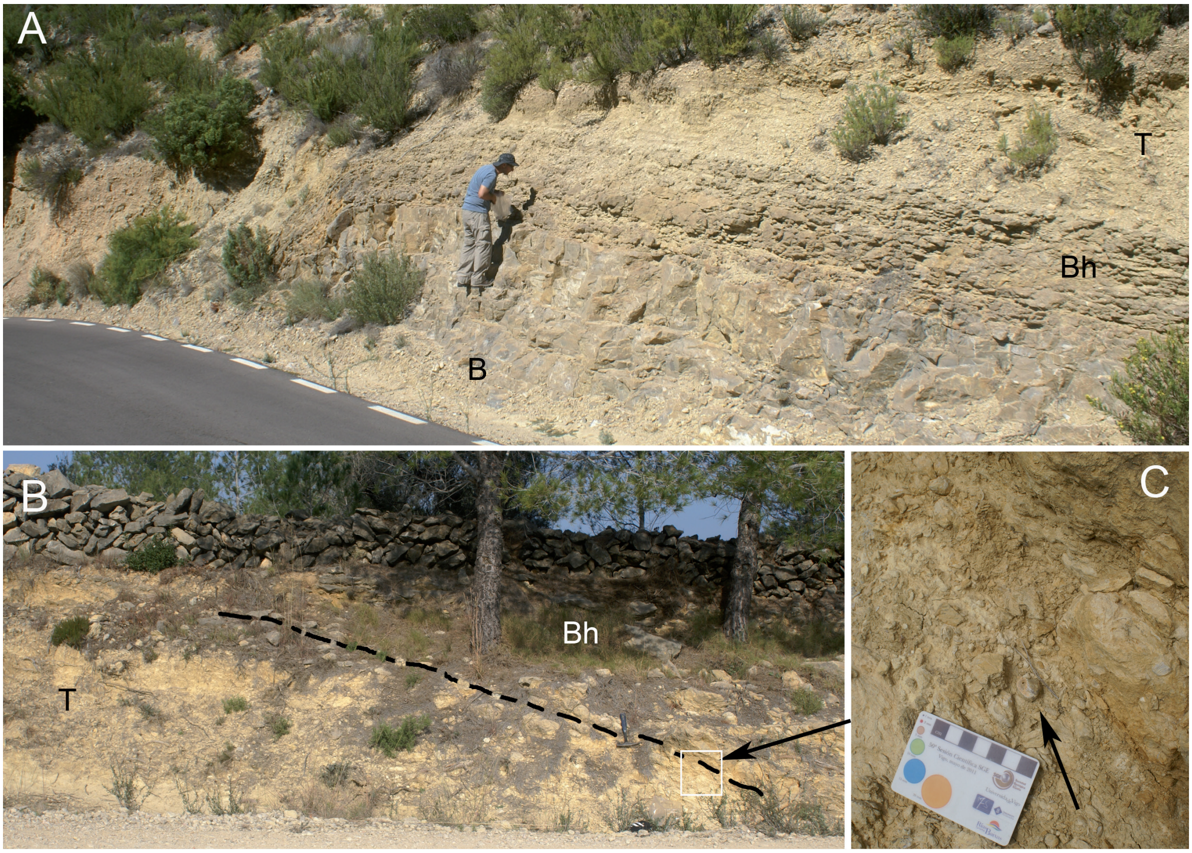


Fig. 3.- Field views of the Lower Jurassic outcropping sections at several localities. A. Lower part of the Sot de Chera section showing the bottom layers consisting of the Barahona Fm. (B), with condensation levels marking an unconformity at the top known as the “*Barahona-hardground*” (Bh), overlaid by the marly beds of the Turmiel Fm. (T). B. Comparable levels in the Racó de Joana section; note the overturned bedding in this section (the top is to the left of the image). C. Detail view of the basal beds of the Turmiel Fm.; black arrow marks a specimen of *Quadratirhynchia attenuata*.

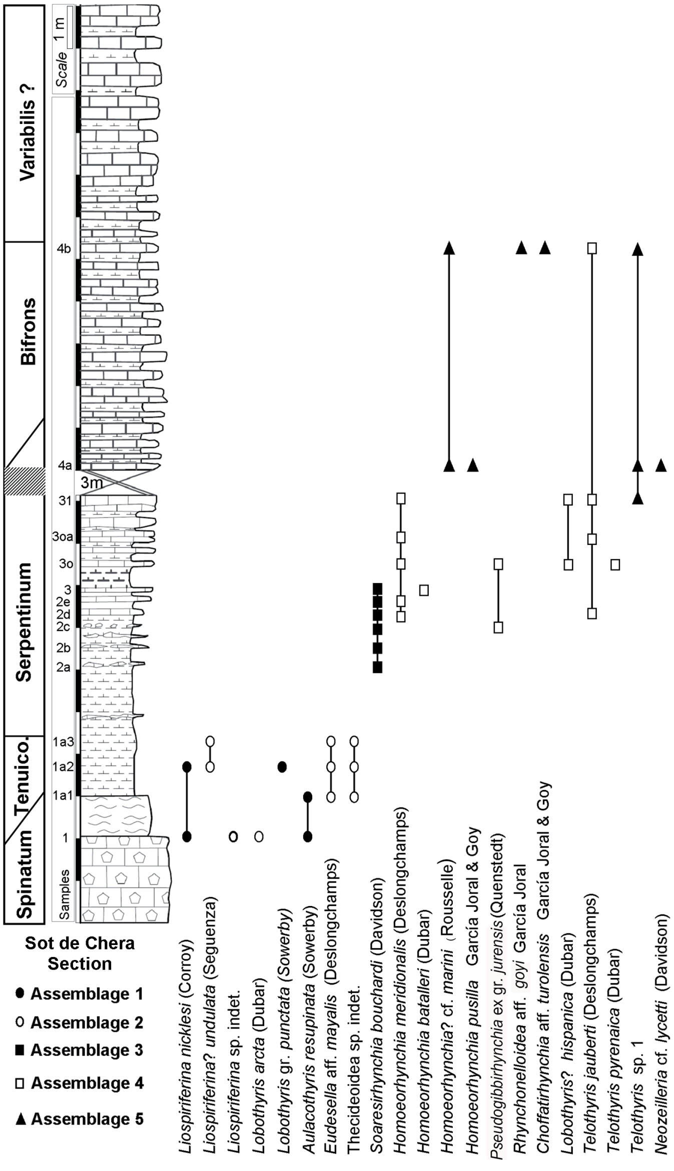


Fig. 4.- Distribution of the assemblages and brachiopod occurrences in the Sot de Chera section.

I-LS, the diversity dynamics of the brachiopod assemblages is markedly conditioned by this event, showing a high diversity in the assemblages but with a discontinuous stratigraphic distribution related with the extinction and recovery phases linked to the ETMEE (Figs. 4, 5).

The analysis of the established assemblages in this area suggests multiple distinctive diversity turnovers and critical brachiopod-based bioevents, which distinguish them from the adjacent palaeogeographic domains:

5.1. Palaeobiogeographical pre-ETMEE affinities

From a palaeobiogeographical standpoint, in the I-LS, taxa exclusively representative from the Mediterranean bioprovince are not recorded prior to the ETMEE. In the Upper Pliensbachian-lowermost Toarcian deposits, except for the thecideid fauna (discussed below), all the species are integrated in the assemblages previously reported from the Iberian Range, which are well established as belonging to the NW-European (Euro-Boreal) epicontinental bioprovince (cf. Ager, 1967, 1971; Delance, 1972; Vörös, 1977, 1984, 2016; García Joral and Goy, 2000; Manceñido, 2002; García Joral *et al.*, 2011) or even have ubiquitous character (*L.* gr. *punctata*, *A. resupinata*). In the adjacent Betic basins, the Mediterranean affinity is evidenced since the late Sinemurian up to the early Toarcian (Baeza-Carratalá and García Joral, 2012; Baeza-Carratalá, 2013). After the extinction, faunal unification occurred indicating a free connection between the Subboreal and Mediterranean bioprovinces in the South-Iberian palaeomargin (Baeza-Carratalá *et al.*, 2011; Baeza-Carratalá, 2013).

Therefore it should be ruled out the allegedly transitional Betic/Iberian palaeogeographical character or even the "Betic" affinity that previous authors attributed to the southernmost outcrops of the I-LS (cf. Bizon *et al.*, 1966; Champetier, 1971), such as Racó de Joana and Benifairó-D.

5.2. Event of proliferation of Liospiriferina? undulata

Liospiriferina? *undulata sensu lato,* including *Spiriferina madagascariensis* (Thevenin, 1908) and probably several species grouped into the genus *Calyptoria* by Cooper (1989) and Alméras *et al.* (2010) are typical and abundant representatives of the assemblages from the Madagascariense Zone of the North-East African and the Middle-East platforms (Thevenin, 1908; Alméras, 1987; Cooper, 1989; Alméras and Mouty, 2001; Chiocchini *et al.*, 2002), reaching in its dispersion North-East Sicily (Seguenza, 1885), and the peri-Iberian platform system in Portugal (Comas-Rengifo *et al.*, 2013), Betic Range (Baeza-Carratalá, 2013; Baeza-Carratalá *et al.*, 2016), Catalonia (Delance, 1969; Calzada, 1979) and the Iberian Range (Rousselle, 1977; Comas-Rengifo *et al.*, 2006; García Joral *et al.*, 2011). In the I-LS of the Iberian Range, this taxon shows the greatest profusion and intraspecific variability among all the peri-Iberian platforms (Fig. 6). The occurrence of *L.*? *undulata* in this region is restricted to a few levels (Figs. 4, 5), probably coinciding with the thermal maximum, just prior to the ETMEE (cf. Gómez and Goy, 2011; García Joral *et al.*, 2011; Baeza Carratalá *et al.*, 2015).

5.3. Thecideid marker horizon

The conspicuous occurrence of several thecideid taxa, most of them consisting of remarkably large-sized specimens (Fig. 8), typifies a regional pre-ETMEE marker horizon ("thecideid beds") which enables correlations among the Lower Jurassic outcrops of the I-LS. Thus far, in the Iberian Range, thecideids are very sparse and have only been occasionally recorded. Mayoral and Sequeiros (1981) figured one specimen from the Toarcian reinterpreted as belonging to thecideids by Manceñido and Damborenea (1990), and Gahr (2002) figured a couple of specimens attributed to *Davidsonella moorei* from

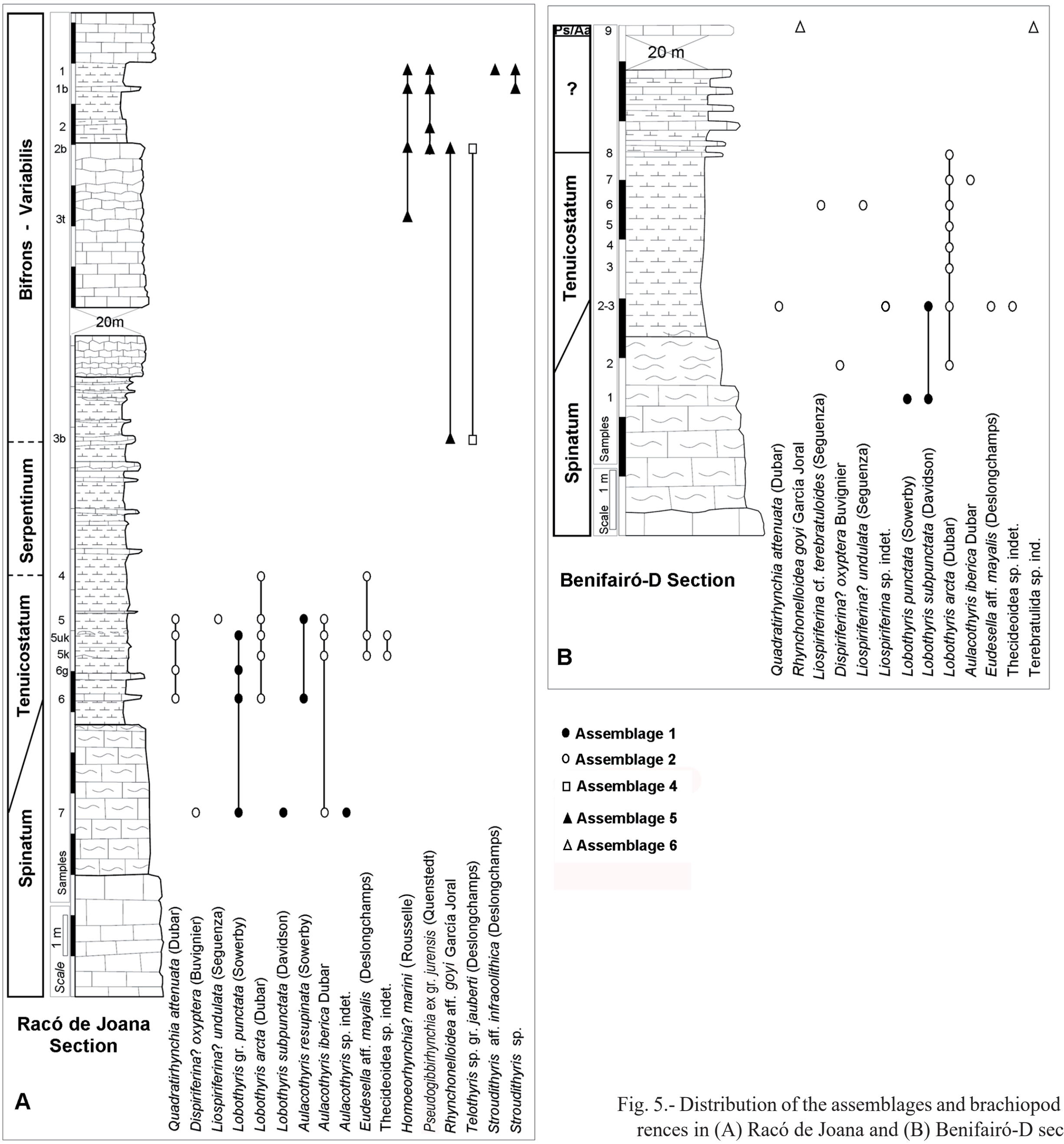


Fig. 5.- Distribution of the assemblages and brachiopod occurrences in (A) Racó de Joana and (B) Benifairó-D sections.

the Aragonese branch of the Iberian Range. Recently, new samplings by one of the authors (FGJ) have also confirmed the occurrence of the group in the Late Toarcian of the Castilian branch of the Iberian Range. There are also undescribed thecideid records in the Oxfordian (Colás Gracia, 2015). All these records of micromorphic thecideids correspond to more recent sediments than the pre-ETMEE "thecideid beds" of the I-LS.

Among the abundant specimens appearing in the thecideid beds, several micromorphic forms could be only uncertainly identified (Thecideida sp. ind.) due to the fragmentary character of the shells and the paucity of the material, making the analysis of their internal structures unfeasible. The prevailing taxon in this assemblage (Fig. 8) has been tentatively assigned to *Eudesella* aff. *mayalis* (Deslongchamps, 1853). The similarity with the type-species of *Eudesella* is evident but some features do not entirely fit into the diagnosis of the Deslongchamps' species, even taking into account the intraspecific variability accepted for this species (Pajaud, 1970).

The Ibero-Levantine representatives of *Eudesella* aff. *mayalis* (Fig. 8) show elongate concavo-convex to plano-convex shells, with a long hinge line and wide and low cardinal areas bearing a well-developed pseudodeltidium. Shells are smooth, with strong growth lines. Pedicle valve is highly convex and thickened, showing the attachment scar on its posterior third. Brachial valve internally shows from 9 to 12 long septa interdigitating with their successive deep lobes. The median septum is stronger and it has attached the closest lateral septum on each side, often developing a central protuberance. Cardinal process is well-developed and at times connected with two lateral ridges. Interior of pedicle valve shows a distinctive subperipheral rim.

This is an unusual fauna in the Western Tethys Ocean as a whole (Fig. 9). Thecideid fauna is only recorded in a comparable stratigraphic situation (though non-conspecific with the Iberian ones) in regions of somewhat higher palaeolatitudes (South England-Normand basins), forming part of the so-called *Leptaena beds* or *Koninckella faunas* (e.g. Davidson, 1851; Deslongchamps, 1853; Moore, 1855), or even in their German counterparts (Rau, 1905).

Referring to the peri-Iberian platforms, in those basins where koninckinid faunas have been reported, such as the Lusitanian basin (e.g. Alméras *et al*., 1988; Comas-Rengifo *et al*., 2013, 2015) or even in the Mediterranean Subbetic area (Baeza-Carratalá, 2013; Baeza-Carratalá *et al*., 2015), thecideids have not been documented as constituents of such assemblage.

5.4. Predominance of the genus Lobothyris in the pre-ETMEE assemblages

Prior to the ETMEE, in the Early Jurassic peri-Iberian platforms system, the Last Occurrence Datum (LOD) of the genus *Lobothyris*, usually typified by *L.* gr. *punctata-L. arcta* never exceeds the LOD of the spiriferinids, which became extinct as effect of the ETMEE (Vörös, 2002; Comas-Rengifo *et al*., 2006). This distribution pattern is clearly evidenced in Asturias and Lusitanian basins (García Joral and Goy, 2009; García Joral *et al*., 2011; Comas-Rengifo *et al*., 2013, 2015) and such groups can be found at most coexisting together in the upper Semicelatum-lowermost Elegantulum subzones from the Aragonese branch of the Iberian Range (García Joral *et al*., 2011).

However, in the I-LS of the Iberian Range, the faunal succession *Lobothyris punctata-L. subpunctata-L. arcta* makes up the prevailing taxa in terms of abundance in the pre-ETMEE assemblages, accounting for nearly 80% specimens and showing an increasing trend representing a bloom in the last pre-ETMEE levels. This bioevent is even more patent in the southernmost outcrops of this region (Racó de Joana and Benifairó-D localities), where *Lobothyris* representatives can be recorded clearly exceeding the LOD of *Liospiriferina*? *undulata* (Fig. 5). After the ETMEE, the genus *Lobothyris* is doubtfully recorded in several localities of the I-LS and the innermost areas of the Iberian Range. It is represented by specimens attributed to *L*.? *hispanica* (Fig. 7), as constituent of the "Spanish Bioprovince" of brachiopods occurring in the Serpentinum-lower Bifrons zones.

On the contrary, the high diversification and radiation underwent by the *Liospiriferina falloti* group and very closely related taxa, which is conspicuous along the Pliensbachian-Toarcian transition virtually throughout the Iberian Range, is not evident in the I-LS, where this group is represented only by very scarce specimens of *Liospiriferina nicklesi* and *L*. cf. *terebratuloides*.

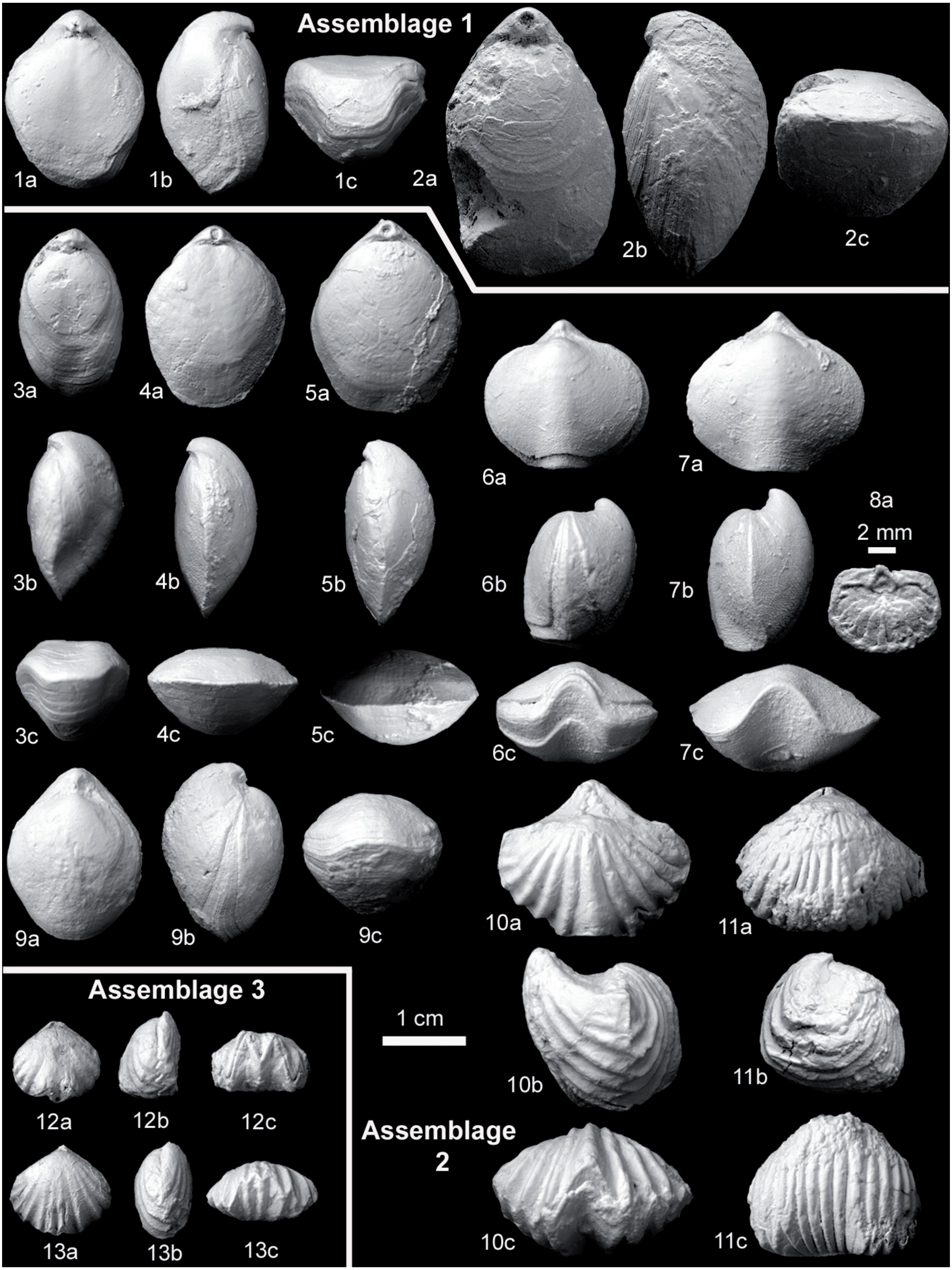
5.5. Soaresirhynchia bouchardi as pervasive post-ETMM opportunistic species

The post-ETMEE pattern of repopulation led by *S. bouchardi,* mainly recorded in the Elegantulum Subzone from many Western Tethyan basins, is distinctive of an opportunistic strategy occupying vacant habitats in both epicontinental (e.g. García Joral and Goy, 2000; García Joral *et al*., 2011; Comas-Rengifo *et al*., 2013, 2015) and epioceanic areas (e.g. Baeza-Carratalá *et al*., 2011; Baeza-Carratalá, 2013) of the peri-Iberian platforms. In the I-LS this pattern is verified, as the onset of the repopulation phase is recorded as monospecific levels of this taxon, which shows abundant populations with high intraspecific variability, including several of the morphotypes classically recognized in this species (Figs. 4, 6). The last horizons containing *S. bouchardi* in this region evidence a transitional record leading to the onset of the overlying Assemblage 4, since *S. bouchardi* temporarily co-occurs with several species of this assemblage (Fig. 4).

5.6. Earlier onset of the Assemblage 5

After the ETMEE, during the Middle-Upper Toarcian and even in the Aalenian, the distribution of the brachiopod faunal successions in the Iberian Range is markedly conditioned by the depositional sequences, particularly by the frequent variations on the bedding thickness and facies (García Joral *et al*., 1990). The transition from the predominantly marly Turmiel Fm. to the carbonate sediments (Casinos Fm.) in the Toarcian occurs earlier in the I-LS than in the remaining regions of the Iberian Range. Thus, the onset of the carbonate facies can be regarded as diachronic (Fig. 2), as it is dated in the Bifrons-Variabilis zones in this sector, while it is dated in the northernmost areas of the basin as Early Bajocian and, in

Fig. 6.- (next page) Some representative species of the Assemblages 1, 2 and 3 from the Ibero-Levantine sector of the Iberian Range. 1, 2: Assemblage 1 from the Spinatum-lowermost Tenuicostatum zones. 1: *Aulacothyris resupinata* (Sowerby), specimen SC1.A1 from Sot de Chera section. 2: *Lobothyris subpunctata* (Davidson), specimen SL7-Ls1 from Racó de Joana section. 3-11: Assemblage 2 from the Tenuicostatum Zone. 3: *Aulacothyris iberica* Dubar, specimen SLU.A1 from Racó de Joana section. 4, 5: *Lobothyris arcta* (Dubar): (4) specimen DB3.Ar1 and (5) DB4.Ar1 from Benifairó-D section. 6, 7: *Liospiriferina*? *undulata* (Seguenza): (6) specimen SL5.Un1 and (7) specimen SL5.Un2 from Racó de Joana section. 8: *Eudesella* aff. *mayalis* (Deslongchamps), specimen SC1a.Em5 from Sot de Chera section. 9: *Liospiriferina* cf. *terebratuloides* (Seguenza), specimen DB6.Te1 from Benifairó-D section. 10: *Dispiriferina*? *oxyptera* (Buvignier), specimen SL7.Ox1 from Racó de Joana section. 11: *Quadratirhynchia attenuata* (Dubar), specimen SLG.At.1 from Racó de Joana section. 12, 13: Assemblage 3. *Soaresirhynchia bouchardi* (Davidson), specimens SC2a.bo1 (12) and SC3t.bo1 (13) from the lowermost Serpentinum Zone of Sot de Chera section. a: dorsal, b: lateral, and c: anterior views, except for 8 (a: internal dorsal view).


Assemblage 1
1a
1b
1c
2a
2b
2c
3a
4a
5a
6a
7a
8a
2 mm
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5b
6b
7b
3c
4c
5c
6c
7c
9a
9b
9c
10a
11a
Assemblage 3
1 cm
10b
11b
12a
12b
12c
Assemblage 2
13a
13b
13c
10c
11c

the north of the Castilian branch, it even corresponds to the Pseudoradiosa Zone (Gómez, 1979).

This premature change in the depositional environment predisposed the earlier record of some constituents making up the Assemblage 5, some of them even showing similar morphotypes to the components forming part of the Assemblage 6 recorded in the Pseudoradiosa-Aalensis zones (e.g. *Rhynchonelloidea* aff. *goyi*). In this sense, García Joral *et al*. (1990) ascertained that, in the Iberian Range, the FOD of *R. goyi* occurs in the upper Pseudoradiosa-lowermost Aalensis zones, but if a steady calcareous sedimentation persists, *R. goyi* can occur up to the uppermost Aalensis Zone.

To some extent, similar conditions could take place in the I-LS, as comparable morphotypes to *R. goyi* (*R.* aff. *goyi*) have been recorded in the first levels of the Casinos Fm. (Figs. 3, 4), with a prevailing calcareous component (Bifrons-Variabilis zones), preceding the "true *R. goyi s.s*.".

Otherwise, *R. goyi s.s*. is recorded in the I-LS in the predominantly grayish limestone upper levels of the Benifairó-D section (Fig. 5), which typifies the Iberian-Mediterranean biogeographic district in the Pseudoradiosa-Aalensis zones (Andrade *et al*., 2016). *R.* aff. *goyi* is distinguished from *R. goyi* for its smaller size and less dense costation, otherwise they are very similar in morphology.

These sedimentological differences can also have influenced the appearance of *Telothyris* specimens with elevated sulciplication (*Telothyris* sp. 1) similar as observed in some species of the genus *Stroudithyris* such as *S. stephanoides* (Fig. 7). These forms are coeval with *Stroudithyris* aff. *infraoolithica,* but can be distinguished from this stock by the more acute sulciplication and by the decisive beak features. *Stroudithyris* representatives show large and oval foramina while they are smaller and rounded in *Telothyris*. We have considered these forms as *Telothyris* sp. 1 because they do not show enough diagnostic criteria to include them in any of the several varieties or species described for this genus.

This homeomorphism agrees with the aforementioned strong influence of the depositional sequences in the basin, as *S. stephanoides* prevails in the calcareous depositional environments from the Aalensis Zone onwards, being replaced by *S. pisolithica* as dominant taxon in more marly deposits (García Joral *et al*., 1990). Maybe, from an anagenetic perspective, this stock might represent a link between the last *Telothyris* species and the earliest records of *Stroudithyris*, but more accurate systematic analysis is required, including some comparable records from different areas and basins.

5.7. Hiatus in the brachiopod record

In the surveyed outcrops, brachiopods are not recorded in the Thouarsense-Dispansum chronozones either due to a stratigraphical gap in the sequences (e.g. Benifairó-D section, Fig. 5) or as results of a barren interval concerning the brachiopod fauna (e.g. Sot de Chera section, Fig. 4). The diversity of brachiopods is also minimal in this interval in other sectors of the Iberian Range, although some taxa have been recorded in localities with more marly sedimentation, such as Ariño or Rambla del Salto (García Joral and Goy, 2004). The next subsequent record in the I-LS corresponds to the Assemblage 6 (Fig. 5), showing lesser diversity in this region than in the northernmost localities from the Iberian Range.

5.8. Under-representation of the Zeilleriidae

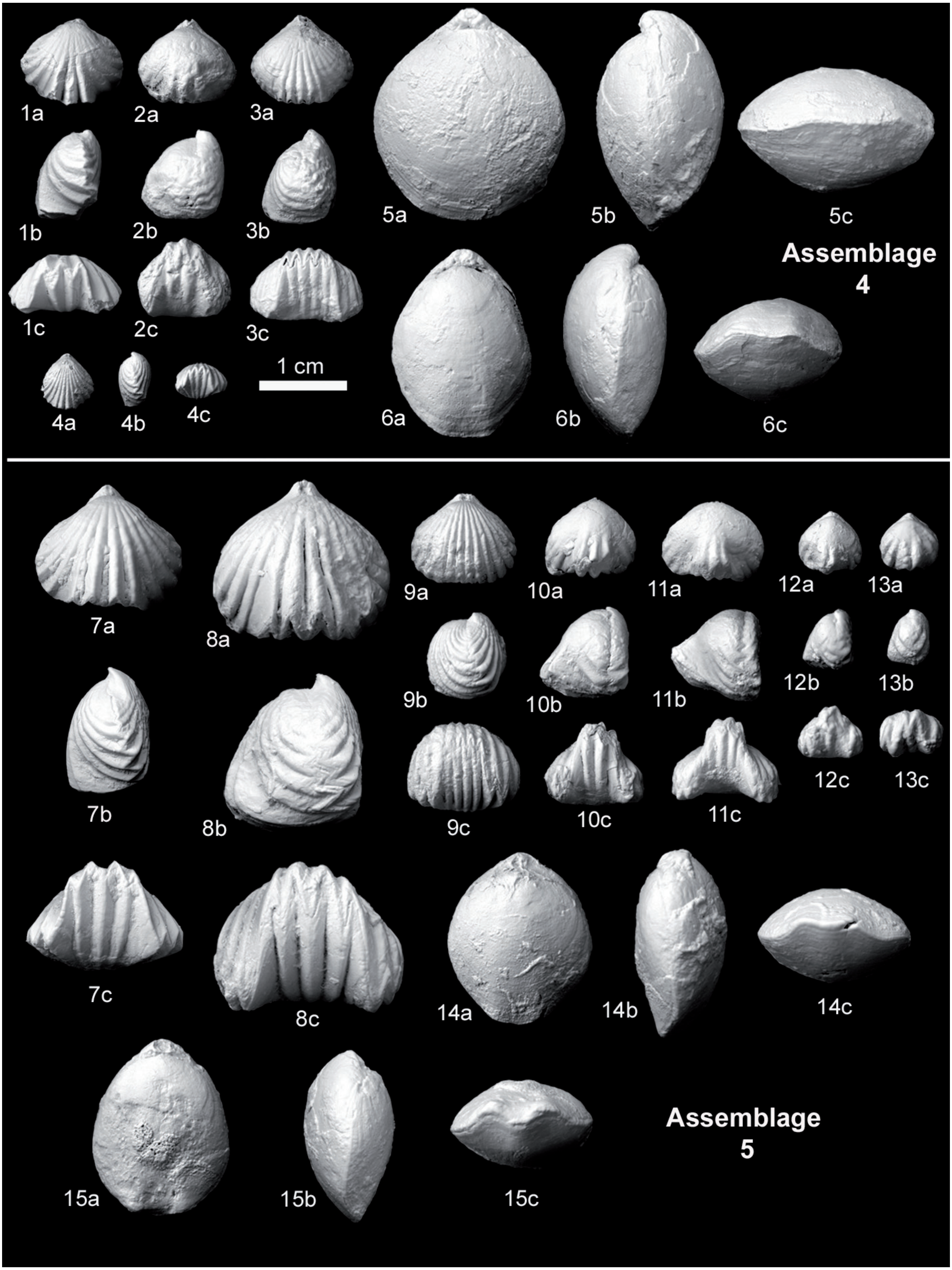
In contrast to the remaining areas of the Iberian Range, zeillerids are scarcely recorded in the I-LS. They are restricted to the species of *Aulacothyris* in the Pliensbachian-Toarcian transition and to the occasional occurrence of a few specimens of *Neozeilleria* cf. *lycetti* in the Assemblage 5. Zeilleriid taxa typify several intervals in diverse northerly localities of the Iberian Range (e.g. *Zeilleria quadrifida, Z. sarthacensis, Z. culeiformis, Aulacothyris blakei*), but they are not recorded in the analysed outcrops probably due to the aforementioned strong influence of the sedimentary conditions. Since, in spite of their virtually homogeneous distribution in the Iberian Range as a whole, they are more conspicuous in shallow marly environments or, at least, with more terrigenous input (cf. García Joral *et al*., 1990).

Southwards, in the neighboring Subbetic area, the pre-ET-MEE zeilleriid record is mainly characterized by *Bakonyithyris, Securina* and several typical Mediterranean species of *Zeilleria* (Baeza-Carratalá, 2013; Baeza-Carratalá and García Joral, 2014), which are not recorded in the I-LS either.

6. Conclusions

Brachiopod fauna in the Late Pliensbachian-Late Toarcian from the Ibero-Levantine sector of the Iberian Range

Fig. 7.- (next page) Some representative species of the Assemblages 4 and 5 from the Ibero-Levantine sector of the Iberian Range. 1-6: Assemblage 4 from the the Serpentinum-lowermost Bifrons zones. 1, 2: *Homoeorhynchia meridionalis* (Deslongchamps): 1, specimen SC30.Hm1 and 2, specimen SC30a.Hm1 from Sot de Chera section. 3: *Homoeorhynchia batalleri* (Dubar), specimen SC3t.Ba1 from Sot de Chera section. 4: *Pseudogibbirhynchia* gr. *jurensis* (Quenstedt), specimen SL2b.Ju1 from Racó de Joana section. 5: *Telothyris jauberti* (Deslongchamps), specimen SC31.Tj1 from Sot de Chera section. 6: *Lobothyris*? *hispanica* (Dubar), specimen SC30a.Hi.1 from Sot de Chera section. 7-15: Assemblage 5 from the Bifrons-Variabilis zones. 7, 8: *Rhynchonelloidea* aff. *goyi* García Joral: 7, specimen SC4b.Afg1 and 8, specimen SCAs5. Afg1 from Sot de Chera section. 9: *Choffatirhynchia* aff. *turolensis* García Joral and Goy, specimen SC4B.Tu1 from Sot de Chera section. 10, 11: *Homoeorhynchia*? *marini* (Rousselle): 10, specimen SC4a.Hm1 from Sot de Chera section; 11, specimen SL1.Hm1 from Racó de Joana section. 12, 13: *Homoeorhynchia pusilla* García Joral and Goy: 12, specimen SC4a.Hp1 and 13, specimen SC4a.Hp2 from Sot de Chera section. 14. *Telothyris* sp. 1, specimen SC4b.Tel1 from Sot de Chera section. 15. *Stroudithyris* aff. *infraoolithica* (Deslongchamps), specimen SL1.Si1 from Racó de Joana section. a: dorsal, b: lateral, and c: anterior views.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Assemblage 4
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8a
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10b
11b
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15c
Assemblage 5

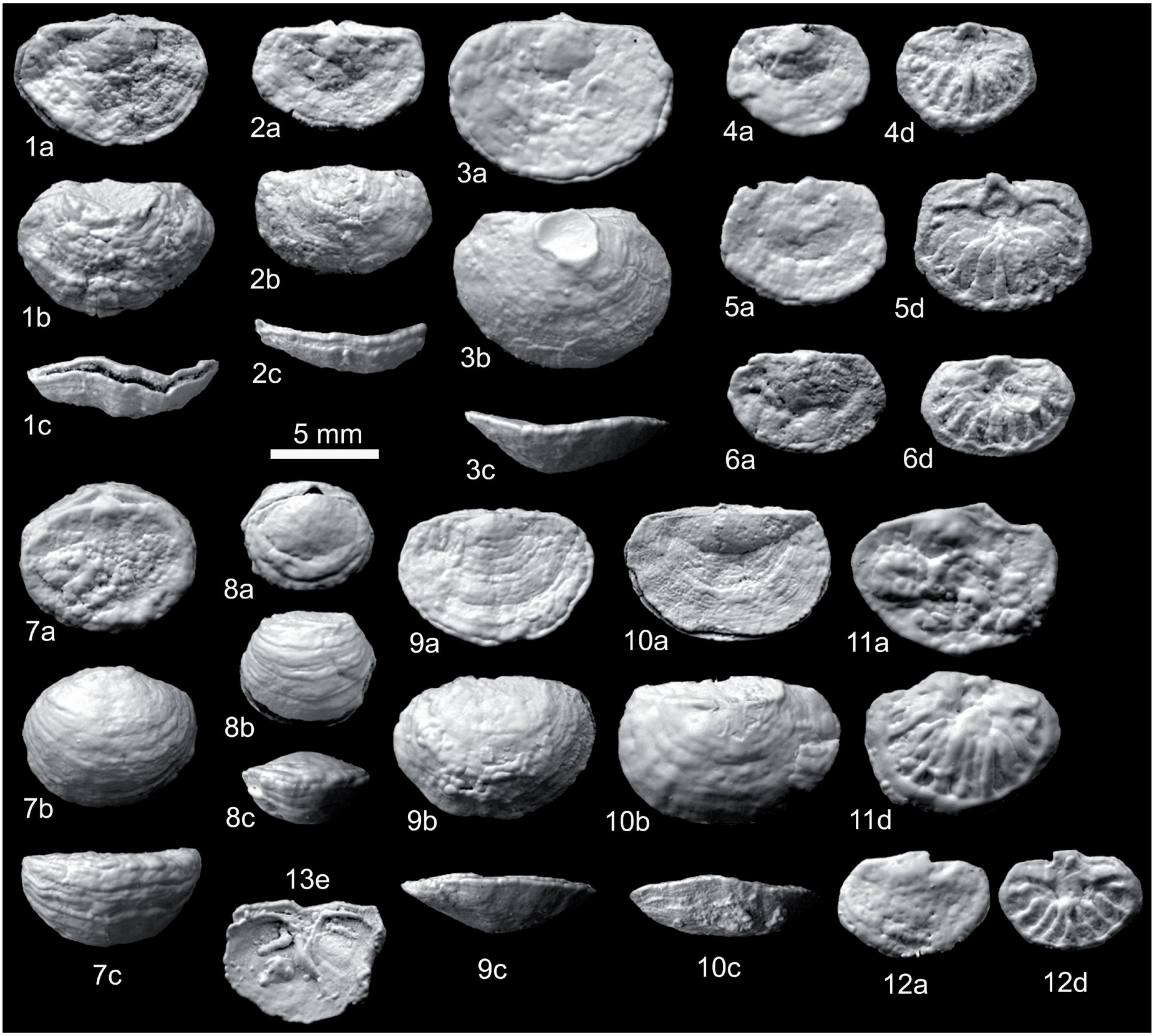

Fig. 8.- Some representative specimens of the "thecideid beds", typifying marker beds in the Assemblage 2 from the Tenuicostatum Zone of the Ibero-Levantine sector of the Iberian Range. 1-6: *Eudesella* aff. *mayalis* (Deslongchamps) from Sot de Chera section: 1. SC1a.Em1 specimen; 2. SC1a.Em2 specimen; 3. SC1a.Em3 specimen; 4. SC1a.Em4 specimen; 5. SC1a.Em5 specimen; 6. SC1a.Em6 specimen. 7, 9-13: *Eudesella* aff. *mayalis* (Deslongchamps), from Racó de Joana section: 7. SL4.Em1 specimen; 9. SL5.Em1 specimen; 10. SL5.Em2 specimen; 11. SL5.Em3 specimen; 12. SL5.Em4 specimen; 13. SL5.Em5 specimen. 8. Thecideida sp. ind. from Racó de Joana section: SL4.Em2 specimen. Images of each specimen are ordered consecutively in (a) external dorsal, (b) external ventral, (c) anterior, (d) internal dorsal, and (e) internal ventral views.

has been arranged for the first time into six assemblages and calibrated with the exhaustively controlled biochronological data available in the Iberian Range. The succession of the assemblages, consisting of 29 species, shows a discontinuous stratigraphic distribution since its diversity dynamics is markedly conditioned by the extinction phases linked to the ETMEE in the region.

The faunal succession shows strong affinities with that recorded in the remaining epicontinental platforms from the Iberian Range, because almost all the species are represented in the NW-European (Euro-Boreal) province, the transitional or even "Betic" (i.e. Mediterranean) palaeogeographical affinity previously attributed to the southernmost part of this region, can be confidently ruled out.

Amidst the main brachiopod-based bioevents must be considered the predominance of the genus *Lobothyris* in the pre-ETMEE assemblages, the conspicuous record of *Liospiriferina*? *undulata* and, especially, the first evidence in the Iberian Peninsula of Jurassic pre-ETMEE thecideid marker beds mostly made up by *Eudesella* aff. *mayalis,* allowing potential correlations with somewhat higher palaeolatitude regions.

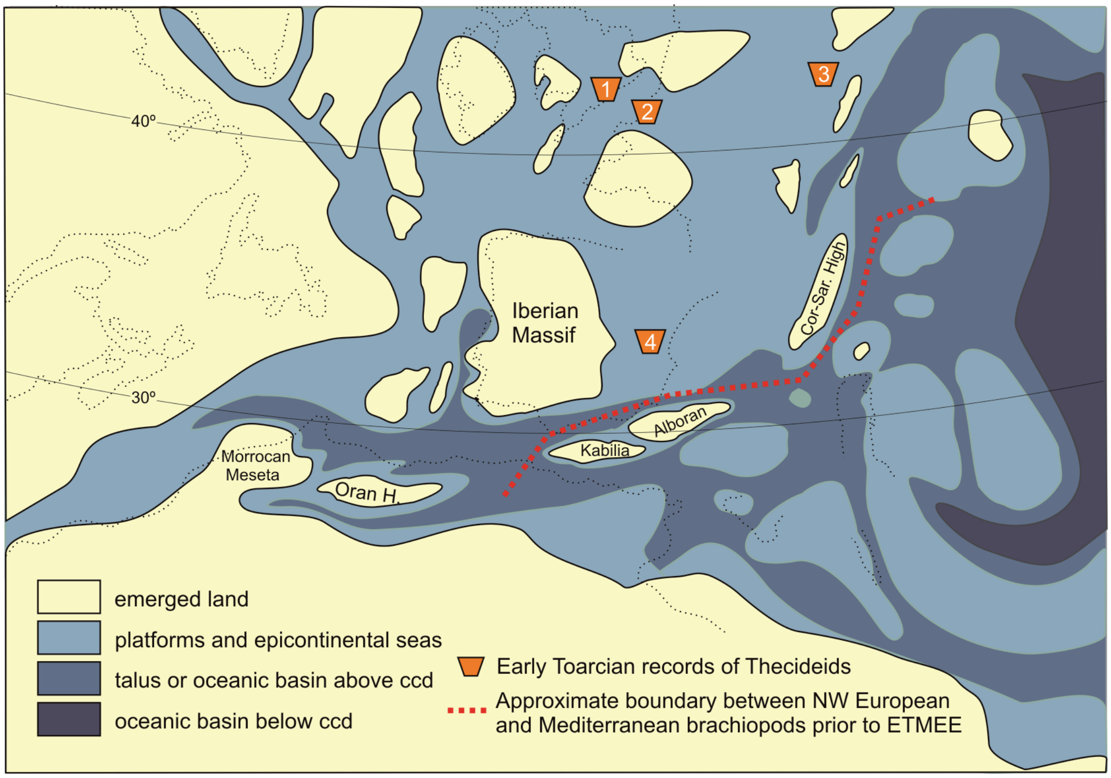

Fig. 9.- Paleogeographical map of the Western Tethys in the Early Toarcian (slightly modified after Bassoullet *et al*., 1993) showing the boundary between brachiopod provinces and the occurrence of Thecideids. 1: South England; 2: Normandy; 3: South Germany; 4: Ibero-Levantine Sector of the Iberian Range.

During the Middle-Upper Toarcian, the distribution of the brachiopod assemblages in the Ibero-Levantine sector is markedly influenced by the depositional sequences, entailing premature turnovers and involving the earlier record of homeomorphic morphotypes of younger terebratulides and rhynchonellides. Sedimentary conditions may have caused the under-representation of zeillerids as well.

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