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Brachiopod faunal exchange through an epioceanic-epicontinental transitional area from the Early Jurassic South-Iberian platform system ✡

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Abstract

The La Mola region (eastern External Betic Zone) can be regarded as one of the easternmost complete Jurassic successions of the Betic Cordillera in the Iberian Peninsula, but the paleogeographical setting of their outcrops remains widely discussed. Analysis of brachiopod assemblages from the Lower Jurassic improves the accuracy of previous paleogeographical data, enabling identification of a mainly epioceanic transitional area in which influences of epicontinental habitats are also detected. Assemblage 1, mainly with a Mediterranean affinity but also sharing several constituents with the African and Northeastern Iberian basins, typifies the Sinemurian-Pliensbachian transition. Assemblage 2, as a whole, shows a transitional character between epioceanic and epicontinental habitats; it is subdivided into two successive and interrelated sub-assemblages: Ass. 2a (Demonense-Tenuicostatum Zones) reveals a free connection with the epioceanic Subbetic area, whereas Ass. 2b (uppermost Pliensbachian-lower Toarcian) shows a closer relationship with epicontinental environments. Assemblage 3 (uppermost Spinatum-basal Serpentinum Zones) is commonly recorded in the peri-Iberian epicontinental platform system integrated within the NW-European bioprovince, but it can also be regarded as a marginal assemblage that is widespread in the westernmost Tethyan margin prior to the Early Toarcian extinction event. Assemblage 2 constitutes a suitable index for assessing the paleobiogeographical affinity of the La Mola region, as Ass. 2a is progressively replaced by Ass. 2b, thus triggering the arrival of epicontinental taxa to the more intra-epioceanic Subbetic environments, inferring a possible connection through the La Mola transitional slope. Consequently, this region enabled a faunal mixing and exchange between both environments, and La Mola likely remained as an area that would facilitate migration and an effective dispersal seaway or, at least, did not constitute an ecological filter-barrier for brachiopods. Biostratigraphical data from brachiopods and ammonites are correlated for the first time in La Mola, refining and calibrating biochronostratigraphical gaps in the pre-Domerian deposits where biochronological markers are usually scarce, and around the Pliensbachian-Toarcian boundary, a crucial timespan in which the Early Toarcian extinction event took place.

Keywords:
Early Jurassic
Brachiopod assemblage
Geographic distribution
Betic Cordillera
Paleobiogeography
Biostratigraphy

1. Introduction

Distribution of benthic organisms with a short planktonic larval stage, such as brachiopods, is widely used as a suitable tool for the establishment of Mesozoic paleobiogeographical biochoremas (Ager, 1967; Vörös, 1984, 1993, 2005; Manceñido, 2002; Baeza-Carratalá et al., 2014). In the Early Jurassic, the brachiopod provinciality of the Western Tethys Ocean was clearly established in two major biochoremas: the NW-European and Mediterranean paleobioprovinces (Ager, 1967, 1971, 1973; Vörös, 1984, 1986, 1993; Manceñido, 2002). This paleobiogeographical distribution has been interpreted by several authors in terms of epioceanic and epicontinental habitats, respectively (cf. Hallam, 1971; Vörös, 1986, 2005; Ager, 1993; Colás and García Joral, 2012; Baeza-Carratalá et al., 2011a, 2014; Baeza-Carratalá and Sepehriannasab, 2014), where environmental factors such as depth, terrigenous input or nutrient availability, among others, played a decisive role in brachiopod settlement. Consequently, epioceanic-epicontinental transitional areas providing evidence of brachiopod migration or faunal exchanges are worth studying in order to throw light upon the development of effective dispersal seaways or, conversely, faunal filter-barriers. In the Betic Cordillera, one of these changeover zones could have developed around the La Mola region (Alicante, Spain), located on the easternmost transitional slope between the Intermediate Domain (between the Prebetic-Subbetic zones) and the Subbetic area (Nieto et al., 1994, 2014; Nieto, 1997).

The present paper attempts to detect possible connections through a transitional area between the epioceanic Subbetic basins and the epicontinental platform system established during the Early Jurassic in the south-Iberian margin by means of taxonomic and paleobiogeographical analyses performed on the brachiopod assemblages from the La Mola region. The paleogeographical setting of the La Mola region during the Jurassic has been widely discussed in earlier studies. Some authors have ascribed this region to the Subbetic domain (Fallot, 1945; Iñesta et al., 1990; Iñesta, 1993), whereas others described it as part of the Intermediate Domain, between the Prebetic and Subbetic areas (Azéma, 1977; Nieto et al., 1994; Nieto, 1997). Our research puts forward a comparative analysis of the brachiopod assemblages from La Mola, thus enhancing the knowledge provided by previous studies (Jiménez de Cisneros, 1920, 1927; Iñesta, 1993). These assemblages are compared with the well documented faunas from neighboring basins such as the Eastern Subbetic (Baeza-Carratalá, 2011, 2013; Baeza-Carratalá and Garcia Joral, 2012), the Iberian Range (García Joral and Goy, 2000; García Joral et al., 2011), the Internal Betic Zones (Baeza-Carratalá et al., 2011a), and the Lusitanian Basin (Comas-Rengifo et al., 2013, 2015). As a result, these analyses provide new data on this transitional region, which can be regarded as the easternmost complete Jurassic succession of the Betic Cordillera in the Iberian Peninsula, as well as the outcrops closest to the epicontinental habitats with brachiopod records, in the absence of the exposure of the Prebetic ones.

Finally, previous ammonite records are combined with the new data provided herein by brachiopod assemblages from the La Mola section and correlated with biochronologically well-documented ones from adjacent basins such as the Subbetic area, Internal Betic zones, Lusitanian basin and Iberian Range. This enabled us to calibrate chronostratigraphical and depositional hiatuses previously identified in this area, contributing to a better understanding of the regional lowermost Jurassic facies where biostratigraphical markers are very scarce (Vera, 1998), as well as the Pliensbachian-Toarcian transition interval in this region, a crucial timespan in which the Early Toarcian extinction event took place in the Tethys Ocean as a whole.

2. Geographical and geological setting

La Mola Hill is an isolated Jurassic outcrop surrounded by Triassic deposits in Keuper facies located in the Western part of the province of Alicante (Fig. 1). It is located to the North of the city of Novelda and can be considered as an intermediate area between the Southern Iberian Range outcrops (Albacete and Valencia), the Balearic Isles, and the Eastern Betic Cordillera. This outcrop presents the easternmost complete Jurassic succession of the Betic Cordillera in the Iberian Peninsula, as there are no outcrops in eastern Alicante or southern Valencia revealing well-developed Betic Jurassic successions. Indeed, only the western Balearic Isles, as the prolongation of the Cordillera, present any appropriate Jurassic sequences (Vera et al., 2004).

Jurassic outcrops in La Mola Hill are embedded within a NNW-SSE diapiric lineation (a salt wall known as the Vinalopó Valley diapir) of Triassic Keuper facies (shales, gypsum, and sandstones). This diapiric lineation separates the Prebetic of the Alicante Domain (De Ruig, 1992) to the East, and the Prebetic *s.s.* and the Subbetic ones to the West (García-Hernández et al., 1980) (Fig. 1). The first one is mainly characterized by thin and poorly known Jurassic dolomite successions overlain by thick marly and calcareous Cretaceous deposits, and mainly reworked facies in the Paleogene sequences. Furthermore, sedimentation in shallow epicontinental platforms prevailed in the Prebetic in the North; southward, the Subbetic was characterized in the Early Jurassic by shallow carbonate platforms and subsequently by pelagic seamount facies during most of the Jurassic and Early Cretaceous (Vera et al., 2004).

La Mola Hill comprises Lower Jurassic-Lower Cretaceous sediments and is surrounded by Triassic Keuper facies (Figs. 1, 2). The earliest Jurassic rocks consist of a massive dolostone sequence (Fig. 2 and 1 in Fig. 3) with an upper irregular top corresponding to a dolomitization front. Above this sequence are outcroppings of massive whitish-creamy wackestone beds (2 in Fig. 3) with benthic foraminifera, brachiopods, and scarce bivalves. The top of these massive limestone beds is overlain with a thick-bedded red crinoidal grainstone sequence, including several erosive top-bed surfaces (Figs. 2, 3). These crinoidal limestone sediments fill up small-perched basins originated by listric faults, and are occasionally reduced to a condensed surface with a thickness of several centimetres (Figs. 2, 3). The top of this interval is marked by a sharp unconformity consisting of a distinctive condensation hardground surface that includes Fe-Mn crusts, belemnites, ammonites, brachiopods, and scarce gastropods and bivalves overlain with a centimetre-thick greyish grainstone bed exhibiting a conspicuous profusion of belemnites (Figs. 2, 3). Nieto (1997) assigned this hardground to the lower-middle Domerian, as a gap between the Gavilán Fm. and the overlying Baños Fm. This surface separates the underlying calcareous interval from the upper yellowish marls and marly limestone beds, the latter showing heterogeneous bedding.

The yellowish marly interval is approximately 14 m thick (Fig. 3); it can be subdivided by a distinctive 2 m-thick marly level, with no calcareous bed intercalations observed in its intermediate part. At the top of this distinctive level, a highly bioturbated reddish level appears, indicating a major contrast with an overlaying well-bedded decimetre-thick whitish micritic limestone succession (7 in Fig. 3). This interval can be compared to similar levels associated with an unconformity assigned to the Early-Middle Jurassic transition in the nearby Sierra del Reclot in the Subbetic area (Caracuel et al., 2004; Baeza-Carratalá et al., 2011b). Finally, the micritic limestone beds changes upwards and laterally to well-bedded whitish dolomites.

3. Material and methods

Brachiopods (124 specimens) were collected from the southern slope of La Mola Hill, where the Lower Jurassic deposits contain the most complete and fossil-rich succession. Sampling in the adjacent quarries provided supplementary partial stratigraphical sections outcropping basal levels. All analyses were performed both at the generic and specific levels. Generic assignments follow the published determinations (mainly from the *Treatise:* Kaesler and Selden, 1997-2007). All specimens are deposited at the *Departamento de Ciencias de la Tierra y del Medio Ambiente* (Alicante University, Spain). Supplementary specimens from La Mola contained in the Jiménez de Cisneros historical collection (Paleontological Museum of Murcia) were analyzed after revision.

The ammonite zonal/subzonal scheme follows the standard scheme proposed by Cariou and Hantzpergue (1997) for the Sinemurian-Toarcian of the Mediterranean Domain; their equivalent in the NW-European Domain has been indicated when correlations were to be performed. We also considered chronostratigraphical data from Azéma (1977), Iñesta (1993) and Nieto (1997) in La Mola, subsequently applying them to calibrate and refine the biochronostratigraphical record.

A paleobiogeographical analysis was performed considering the diversity and representation of the brachiopod species from the La Mola assemblages (from both total number and percentage of shared species viewpoints) with respect to a dataset including several epicontinental *vs*. epioceanic environments, particularly from the peri-Iberian platform system and nearby basins. The occurrence of common/closely related species was also taken into consideration, comparing the material from La Mola with representative areas of the

Western Tethys. Some of them were then plotted on paleomaps slightly modified from Bassoullet et al. (1993). The base map employed to illustrate the faunal exchange in the transitional areas around the Intermediate Domain was redrawn and slightly modified from Vera (1998). The schematic model of the sea bottom physiography of the South Iberian paleomargin during the Jurassic was modified after Olóriz et al. (1996), using a magnified vertical scale in order to better visualize the distinction between epicontinental and epioceanic habitats.

4. Results

4.1. Compositional analysis of the brachiopod-bearing levels and stratigraphical distribution

The lowermost brachiopod-bearing levels derive from the whitish wackestone beds (Fig. 3) which are overlying the basal sequences of the Lower Jurassic dolomite succession. Several beds have been prospected, accurate sampling being impossible due to the limestone fabrics. Consequently, in most cases determinations were only feasible over the outcrops, and specimens tended to be fragmentary (Fig. 4).

These basal levels are dominated by the occurrence of multicostate rhynchonellids such as *Gibbirhynchia curviceps* (Quenstedt), *Quadratirhynchia crassimedia* (Buckman), *Calcirhynchia plicatissima* (Quenstedt), *Prionorhynchia regia* (Rothpletz), and both smooth (*Liospiriferina alpina* (Oppel), *Cisnerospira* aff. *adscendens*) and ribbed (*Dispiriferina*? *segregata* (Di Stefano)) spiriferinids (Fig. 4). Occasional undeterminable zeilleriids are present in these beds but are not recorded upwards in the section (Fig. 3). There is a noteworthy presence of *C.* aff. *adscendens*, which appears to be endemic to the Betic area (Baeza-Carratalá et al., 2011a). *Dispiriferina*? *segregata* unusually shows four ribs in the ventral sulcus rather than the 2-3 commonly known ones, as a result of bifurcation.

Overlying this succession, brachiopods are recorded in the red crinoidal grainstone beds. All previous brachiopod reports from the La Mola section documented as fossil nests (Jiménez de Cisneros, 1920, 1927; Iñesta, 1993) derive from this lithostratigraphical unit. Brachiopods are patchily distributed, but at least three biochronostratigraphically different levels with brachiopod fauna can be distinguished within this unit (Fig. 3). In the lowermost layers, the faunal content consists of *Q. crassimedia*, *Prionorhynchia* cf. *flabellum* (Gemmellaro), *Cirpa briseis* (Gemmellaro), *Liospiriferina rostrata* (Schlotheim), *L. alpina*, *Cisnerospira angulata* (Oppel), *Lobothyris* cf. *edwardsi* (Davidson), *Linguithyris aspasia* (Zittel), and *Phymatothyris* sp. indet.

In the hardground located into the crinoidal grainstone succession and subsequent strata, just below the upper hardground at the top of this litostratigraphical unit (Fig. 3), there is a predominance of *Lobothyris* cf. *edwardsi* and *Lobothyris* sp. 1. The aforementioned spiriferinid taxa (*L. rostrata, L. alpina, C. angulata*) occur together with *Liospiriferina obtusa* (Oppel). Within the genus *Prionorhynchia*, *P. gignouxi* (Jiménez de Cisneros) replaces all previously recorded species, and *Cirpa briseis* (particularly large-sized in these beds) is jointly recorded with *Cirpa* aff. *latifrons*. A single juvenile specimen was split from *C. briseis* and assigned to *Cirpa* aff. *latifrons* because of its flatter valves and the distinctive ribbing pattern, with bifurcate ribs even discernible at the earlier stages.

One can deduce an evident correlation between the levels sampled by Iñesta (1993) and the red crinoidal grainstone unit in the present study, given that all taxa previously reported by this author are included in the faunal content provided herein. Hence, *Lobothyris* cf. *edwardsi* was attributed to *Terebratula* sp. 1 and *T.* sp. 2, and *Prionorhynchia gignouxi* to *Rhynchonella* sp. by Iñesta (1993).

One of the most problematic topics in this fauna clearly involves the distinction among the smooth terebratulids belonging to the *Lobothyris* genus since, considering the intraspecific variability and morphological plasticity of some taxa assigned to this genus, it is difficult to establish consistent taxonomic criteria for distinguishing them. Some previous authors have established functional criteria mainly based on shell outline and the features of the beak and pedicle foramen (Alméras and Fauré, 2000, 2007; García Joral et al., 2011). This type of criteria enabled us to classify large-sized specimens with a subpentagonal outline, both valves thicker and a box-like anterior view, all arranged within *Lobothyris* cf. *edwardsi*. The type of this species (Davidson, 1851) and specimens recorded from the Iberian Range (García Joral et al., 2011) differ from those recorded in the La Mola section in that they present more erect beaks, thus showing a narrower symphytium.

Moreover, smaller-sized specimens exhibiting straight posterior edges, a widening outline in the anterior third of the shell and both beak and pedicle foramina proportionally smaller, are cautiously regarded as *Lobothyris* sp. 1. These forms can be clearly split from the typical *L. punctata*-*subpunctata* stock, which is characterized by larger shells, a prominent beak and a subelliptical outline. *Lobothyris* sp. 1, recorded herein within the Margaritatus Zone, could have spread to the Portuguese platforms during the Spinatum-basal Tenuicostatum Zones, as specimens with a similar outline and external features have been reported as *L. subpunctata* from Peniche (Comas-Rengifo et al., 2015) and *L. arcta* from Rabaçal (Comas-Rengifo et al., 2013). Additionally, from an anagenetic conception of the genus *Lobothyris* (*sensu* Alméras and Fauré, 2007), this stock fits properly between the typical *Lobothyris punctata-subpunctata* group, widely recorded in the Pliensbachian Tethyan basins, and the more rounded *Telothyris* species, recorded in the uppermost early and middle Toarcian. As a result, *Lobothyris* sp. 1 could be even regarded as a new species, but a accurate systematic analysis is required, including comparison of these forms with those recorded in areas in which this taxon is better represented, such as Portugal.

The last occurrence of brachiopod fauna is recorded in the basal layers above the onset of the marly sedimentation (Fig. 3). The nearly ubiquitous *L. rostrata* is jointly recorded with *Lobothyris* cf. *arcta* (Dubar) and *Liospiriferina undulata* (Seguenza). Although in these levels the specimens are rather poorly preserved, it was possible to attribute some individuals to *L. undulata* due to their small- to medium-sized shells with a clear dorsal uniplication, wider than long, and a very faint capillation. Finally, *Lobothyris* cf. *arcta* shows an oval-elongate outline and a slightly arcuate lateral commissure, also revealing smaller shells than the *L. punctata-subpunctata* group.

4.2. Structure of the brachiopod assemblages

The brachiopod assemblages from the La Mola section can be arranged into three major groups:

- **Assemblage 1** occurs at the bottom of the La Mola section within the whitish wackestone deposits (Fig. 3). It comprises *Gibbirhynchia curviceps*, *Calcirhynchia plicatissima, Prionorhynchia regia*, *Quadratirhynchia crassimedia*, *Dispiriferina*? *segregata*, *Liospiriferina alpina*, and *Cisnerospira* aff. *adscendens* (Fig. 4);
- **Assemblage 2** is recorded in the red crinoidal grainstone beds and is dominated by large-sized multicostate rhynchonellids, *Lobothyris* specimens, and smooth-shelled spiriferinids (Fig. 4). This assemblage can be subdivided into two successive and interrelated sub-assemblages (Ass. 2a and Ass. 2b) with paleogeographical implications (Figs. 3, 4). **Assemblage 2a** consists of *Cirpa briseis*, *C.* aff. *latifrons*, *Prionorhynchia gignouxi*, *P.* cf. *flabellum*, *Quadratirhynchia*? *crassimedia*, *Liospiriferina alpina*, *L. obtusa*, *L.* cf. *rostrata*, *Cisnerospira angulata*, and *Linguithyris aspasia*. **Assemblage 2b** includes *Quadratirhynchia*? *crassimedia*, *Liospiriferina* cf. *rostrata*, *L. alpina*, *Lobothyris* cf. *edwardsi*, and *Lobothyris* sp. 1;
- **Assemblage 3** occurs just at the onset of the marly sedimentation in the basin. Brachiopod fauna is very scarce and difficult to identify. Only poorly preserved

specimens attributable to *Liospiriferina* cf. *undulata, L. rostrata* and *Lobothyris* cf. *arcta* are represented in this assemblage (Fig. 4).

5. Discussion

5.1. Biostratigraphical significance of the brachiopod assemblages

The different brachiopod assemblages identified in the La Mola section are particularly significant from both biochronostratigraphical and paleobiogeographical points of view.

Assemblage 1 can be correlated with the one that typifies the uppermost Sinemurian-lower Pliensbachian deposits (Raricostatum-Aenigmaticum Zones) from the Subbetic area (Baeza-Carratalá and García Joral, 2012; Baeza-Carratalá, 2013), as the combined acme of *G. curviceps, C. plicatissima* and *P. regia* are considered as especially representative bioevents in this timespan, and the remaining taxa of this assemblage are fully included as accompanying species in the Subbetic basin. Some Subbetic bed-markers such as multicostate zeilleriids or several Betic endemic taxa (Baeza-Carratalá, 2011) are not recorded in Assemblage 1, but others such as *Cisnerospira* aff. *adscendens*, only recorded hitherto in the Subbetic and the Internal Betic Zone (Baeza-Carratalá et al., 2011a; Baeza-Carratalá, 2013) are also present in La Mola.

The taxa making up Assemblage 2 are representative of the late Pliensbachian-earliest Toarcian timespan in several peri-Iberian basins such as the Subbetic Domain, Internal Betic Zone, Iberian Range and Portugal. This assemblage can be subdivided into two successive and interrelated sub-assemblages (Ass. 2a and Ass. 2b) which are jointly recorded in the La Mola section, but the distribution range of their constituent taxa is successively replaced. Indeed, the index taxa of Ass. 2a are more abundant in the lower beds, while those of Ass. 2b typify the upper levels (Fig. 3), thus providing them with biostratigraphical and biogeographical connotations.

All brachiopod occurrences contained in the Lower Jurassic deposits from La Mola reported by previous authors (Jiménez de Cisneros, 1927; Azéma, 1977; Iñesta, 1993) can be integrated in Assemblage 2. Biostratigraphical data provided by such authors, mainly based upon ammonites, contribute to calibrating this assemblage. Thus, Jiménez de Cisneros (1927) reported a brachiopod fauna that can now be mostly arranged in Assemblage 2, together with abundant ammonites, significantly including the biochronological marker *Fuciniceras cornacaldense* (Tausch) from the lowermost upper Pliensbachian (Lavinianum Zone, Cornacaldense Subzone). Likewise, Azéma (1977) recorded a brachiopod fauna in the same levels together with *Fuciniceras cornacaldense, F. ambiguum* (Fucini), *F.* cf. *portisi* (Fucini), *Arieticeras micrasterias* (Meneghini), *A.* cf. *fucinii* (Del Campana), and *Litoceras* sp., attributable to the early-middle Domerian (upper Pliensbachian). Moreover, Iñesta (1993) found the foremost faunal constituents of Assemblage 2 together with *Arieticeras bertrandi* (Kilian), *Leptaleoceras canavarii* (Fucini), *L. ugdulenai* (Canavari), *Amaltheus margaritatus* (Monfort), and *Protogrammoceras* sp., thus supporting a late Pliensbachian age (Algovianum Zone, Bertrandi Subzone).

The species making up Assemblage 2a are recorded as forming part of a wider assemblage from the Eastern Subbetic area (Baeza-Carratalá, 2013) which ranges from the early Pliensbachian Demonense Zone to the earliest Toarcian (Tenuicostatum Zone). Likewise, in the Internal Betic Zone, a similar assemblage is recorded jointly with a well-calibrated ammonite fauna (Baeza-Carratalá et al., 2011a) from the uppermost Pliensbachian (Algovianum-Emaciatum Zones, mainly from the Solare-Elisa Subzones). In this assemblage, taxa with a wide biostratigraphic range, such as the spiriferinid species, are found together with *Prionorhynchia gignouxi* and *Cirpa* aff. *latifrons* and are distinctively restricted to the late Pliensbachian. In this sense, *P. gignouxi* is mainly restricted to the Domerian deposits from the Betic Cordillera (cf. Alméras et al., 1993; Baeza-Carratalá et al., 2011a; Baeza-Carratalá, 2013), and *C.* aff. *latifrons* appears to constitute a representative Pliensbachian species from the Subbetic Basin. The latter nominal species has been proposed to design a stock of multicostate rhynchonellids, homeomorphic but definitely unrelated with *Rhynchonella latifrons* (Geyer, 1889), which clearly indicates an internal structure unconnected with that of the genus *Cirpa* (De Gregorio, 1930), being designed as the type species of the genus *Jakubirhynchia* by Tomasových (2006).

The counterparts of Assemblage 2b are found in several basins of the peri-Iberian platform system such as the Iberian Range and the Lusitanian Basin. Accordingly, *L.* cf. *edwardsi* from the La Mola section can be regarded as a form close to *L. edwardsi* from the Iberian Range. The taxa of the Iberian assemblage are also very closely related to those of the La Mola region such as several representatives of the *Liospiriferina* genus, *Quadratirhynchia* species and constituents of the *Lobothyris subpunctata* group *s.l.*, which together form, among others, a typical assemblage recorded in the Spinatum-Tenuicostatum Zones (Assemblage 1 in García Joral and Goy, 2000 and García Joral et al., 2011). Similarly, in Portugal, *Lobothyris* sp. 1 is likely recorded in Rabaçal-Condeixa as *Lobothyris arcta* in the Tenuicostatum Zone (Comas-Rengifo et al., 2013) and in Peniche as *L.* cf. *arcta* together with *Lobothyris edwardsi*, some representatives of the *L. punctata-subpunctata* group, *Cisnerospira* sp., and *Liospiriferina* spp. (among others) around the Pliensbachian-Toarcian boundary, within the Elisa-Mirabile Subzones.

Assemblage 3 is representative of the Lower Toarcian deposits within a wide area of the Western Tethys. In the Iberian Range, *Lobothyris arcta* (Dubar) and *Liospiriferina undulata* are the most representative taxa of an assemblage recorded in the Tenuicostatum Zone, although some of their components can first occur in the uppermost Spinatum Zone (García Joral et al., 2011). *Liospiriferina undulata* is mainly restricted to the Semicelatum Subzone, very close to the ETOAE (Goy et al., 1997; García Joral and Goy, 2000; Comas-Rengifo et al., 2006; García Joral et al., 2011). In the Lusitanian Basin, *L. undulata* is also recorded in the basal Serpentinum Zone, just prior to the ETOAE (Comas-Rengifo et al., 2013). *Lobothyris arcta* is also recorded in the Tenuicostatum (Paltus-Semicelatum Subzones)-Serpentinum Zones (Elegantulum Subzone) in Western Algeria (Elmi et al., 2006; Alméras and Fauré, 2007) and in the Tenuicostatum Zone in the Pyrenees (Alméras and Fauré, 2000). Similarly, in the neighboring Subbetic basin, *Lobothyris arcta* and *Liospiriferina undulata* are the faunal core of an assemblage whose distribution ranges from the uppermost Pliensbachian up to the lowermost Toarcian (Polymorphum Zone).

5.2. Paleobiogeographical affinities of the La Mola assemblages

5.2.1. Paleogeographical setting

As a consequence of the late Sinemurian-Pliensbachian drowning of a wide shallow shelf, a platform system was distributed around the Iberian Massif during the Pliensbachian-early Toarcian onward, constituting the epicontinental habitats of the Iberian Range, Pyrenees, Lusitanian Basin, Algarve, Asturian and Basque-Cantabrian Basins, among others (e.g., Aurell et al., 2002; Vera et al., 2004). The southernmost epicontinental area in this mainly shallow platform system was the Prebetic Zone, which connected southwards with the epioceanic Subbetic habitats established in the South Iberian paleomargin, between the Iberian Plate and the Mesomediterranean microplate (Figs. 5, 6), which subsequently became part of the Internal Betic Zones (García-Hernandez et al., 1980; Martín-Algarra et al., 1992; Vera, 1998, 2001; Vera et al., 2004). The connection between the epicontinental platform system and the Subbetic epioceanic habitats has conventionally been proposed through deeper transitional areas referred to as the Intermediate Domain, although some authors include these areas within the Subbetic pelagic facies.

In this sense, the paleogeographical setting of the La Mola region in the Jurassic is controversial due to its attribution as part of the Subbetic domain (Fallot, 1945; Iñesta et al., 1990, Iñesta, 1993), whereas more regional and comprehensive studies ascribed it to the intermediate zones between the Prebetic and Subbetic areas (Azéma, 1977). It was finally attributed to the transitional slope between the epioceanic External Subbetic and the Intermediate Domain trough (Nieto et al., 1994, 2014; Nieto, 1997), with the epicontinental Prebetic platforms to the north. These authors proposed such a paleogeographical position mainly on the basis of facies analyses from the Toarcian-Aalenian boundary onward. Additional data based on the Early Jurassic brachiopod assemblages can now help to support the paleogeographical evolution of this part of the External Betic Zones.

5.2.2. Paleobiogeographical analysis

The brachiopod provinciality in the Western Tethys during the Early Jurassic is mainly established in two major biochoremas: the NW-European and the Mediterranean bioprovinces (Ager, 1967, 1971, 1973; Vörös, 1984, 1986, 1993; Manceñido, 2002). This paleobiogeographical distribution has been interpreted by several authors in terms of epioceanic and epicontinental habitats, respectively (Hallam, 1971; Vörös, 1986, 2005; Ager, 1993; Colás and García Joral, 2012; Baeza-Carratalá et al., 2011a, 2014; Baeza-Carratalá and Sepehriannasab, 2014), where environmental factors such as depth, terrigenous input or nutrient availability (among others) played a decisive role in brachiopod settlement. Comparison of species diversity and relative abundances from the La Mola assemblages with several epicontinental *vs*. epioceanic environments, especially from the peri-Iberian platform system and nearby basins, enables their biogeographical affinity to be established (Table 1).

Assemblage 1 mainly shows Mediterranean affinities, sharing all the recorded taxa with the Eastern Subbetic assemblages (Baeza-Carratalá, 2013) and presenting a high proportion of species also present in the Internal Betic Zone (57.1%) and in the Bakony region (42.8 %) (Vörös and Dulai, 2007; Vörös, 2009); the latter area is contrasted as a characteristic Mediterranean locality. These affinities are also evident in relation to other neighboring basins such as NW Algeria (Alméras et al., 2007) and the Pyrenees (Alméras and Fauré, 2000). This affinity is weaker when compared with the localities closest to La Mola region, typically belonging to the NW-European province, such as the Iberian Range (Comas-Rengifo, 1982), and presents the minimum percentage of shared species (14.2%) when compared with the Lusitanian Basin (Table 1). There is, however, a remarkable absence in La Mola of Mediterranean biogeographical indicators such as multicostate zeilleriids, which are present in the nearby Subbetic Basin (Baeza-Carratalá and García Joral, 2012).

Assemblage 2, as a whole, shows a transitional character between the epioceanic and epicontinental environments. Actually, the paleobiogeographical affinity varies only slightly (41.7-50%) in most of the basins evaluated (Table 1). Proximity to the Subbetic areas leads to a maximum affinity (83.3%), while the similarity with the adjacent peri-Iberian basins mainly results from the cosmopolitan species and typical boreal taxa (25% with the Lusitanian Basin; 33.3% with the Iberian Range).

Within this Assemblage 2, two groups with paleogeographical connotations (Mediterranean *vs*. NW-European) are continuously mixed (Ass. 2a and 2b). Assemblage 2a reveals a full correlation with the Subbetic assemblages, interpreted in terms of free connection with this area. In the levels where this sub-assemblage is predominantly recorded (lower beds of the red crinoidal grainstone succession), boreal influences are only slightly detected through the occasional occurrences of *L*. cf. *edwardsi* and *Q. crassimedia*. On the other hand, several taxa considered as typically Mediterranean (*L. aspasia*, *Prionorhynchia* spp.) are more abundant in these levels. Slightly more distant basins such as the Internal Betic Zones (Baeza-Carratalá et al., 2011a), the African margins, or the typical Mediterranean Bakony region, which is more distant, show assemblages also related to those from La Mola (50-60% of shared species). Similarly to the previous assemblage, affinity decreases when Ass. 2a is compared with the NW-European basins, except for the Pyrenees (50%), exhibiting the minimum similarity with the Lusitanian Basin (10%). There is also noteworthy supraspecific similarity with the Portuguese assemblages; thus, for instance, *C. briseis, Q. crassimedia* or *P. gignouxi* recorded in La Mola were replaced by more subboreal species such as *C. fallax*, *Q. quadrata* and *P. serrata,* reported by Comas-Rengifo et al. (2015).

Assemblage 2b shows a high affinity with the Eastern Subbetic and the Internal Betic Zones, but also with more epicontinental environments such as the Iberian Range, the Lusitanian Basin and Algeria and the Pyrenees (60%). The lowest percentage is obtained with classical Mediterranean localities such as Bakony (Table 1). Furthermore, *L. edwardsi* is properly considered as a NW-European taxon, as it was defined in Ilminster by Davidson (1851) and then reported in the Iberian Range and Portugal (García Joral and Goy, 2000; García Joral et al., 2011; Comas-Rengifo et al., 2015) (Fig. 5). This taxon is only occasionally recorded in the lower levels where

Assemblage 2 occurs, but it is (together with *Lobothyris* sp. 1) progressively more abundant in the upper levels of the crinoidal grainstone succession, typifying the Ass. 2b group, instead the occasional Mediterranean taxa.

Finally, except for the single record of *L. undulata* from Sicily (Seguenza, 1885), no representative taxa of Assemblage 3 (*Lobothyris arcta* and *Liospiriferina undulata*) have been described in the core areas of the Mediterranean province, such as Bakony or the Southern Alps, which suggests very limited relationships with these areas at that time. Assemblage 3 is therefore clearly better recorded in the NW-European bioprovince, fully coinciding with the assemblages reported from the peri-Iberian platform system integrated into the NW-European province (García Joral and Goy, 2000; Gahr, 2005; García Joral et al., 2011; Comas-Rengifo et al., 2013). This assemblage, however, is also detected in the Subbetic domain (Baeza-Carratalá, 2013) and in the African margins (Alméras et al., 2007) and can be regarded as a marginal assemblage inhabiting the westernmost Tethyan areas prior to the ETOAE (Fig. 5), where biogeographical provincialism between Sub-boreal and Mediterranean provinces was interconnected from the late Pliensbachian-early Toarcian onward (Baeza-Carratalá, 2013).

5.3 Brachiopod faunal exchange through the La Mola transitional area

The paleobiogeographical analysis reveals that the transitional character (epicontinental/epioceanic) in the brachiopod fauna from La Mola is evident since Assemblage 1. Nevertheless, it is the Assemblage 2 (with its corresponding Ass. 2a and Ass. 2b) which provides the most appropriate approach for establishing the biogeographical and paleogeographical evolution of this part of the External Betic Zones in relation to brachiopod fauna, as this assemblage is recorded subsequent to the differentiation of the epicontinental *vs*. epioceanic environments in the Betic Cordillera (Fig. 6). Ass. 1 is recorded around the preceding pre-rifting stage (*sensu* Vera, 1988, 1998; Molina et al., 1999), which produced the incipient compartmentalization of the platform simultaneously with the remaining Western Tethys shelves (Vera et al., 2004). Ass. 3 is recorded with the onset of the marly sedimentation, in a timespan in which a probable unification of brachiopod fauna took place (Baeza-Carratalá, 2013).

Assemblage 2a is progressively replaced by Ass. 2b in the La Mola section (Fig. 3), mainly dominated by the *Lobothyris* group, which is highly distinctive in the epicontinental NW-European assemblages. Conversely, typical Mediterranean terebratulid stock typified by sulcate and axiniform taxa, recorded in Bakony or even in the Subbetic area, such as *Rhapidothyris, Securithyris, Securina, Linguithyris,* or *Viallithyris* (Ager, 1971; Vörös, 1984, 1993, 2005; Manceñido, 2002; Baeza-Carratalá, 2013), are missing in Ass. 2b. Only the pervasive *L. aspasia* is partly co-occurring in the first levels within Ass. 2a, but it is not subsequently recorded upward in Ass. 2b. This evidence suggests a closer relation of Ass. 2b with those of the epicontinental environments than with the fauna habitually recorded in epioceanic habitats.

As for the potential biogeographical marker-beds of this interval, the koninckinid fauna present in the Subbetic basin around this timespan (Baeza-Carratalá et al., 2015), and subsequently in Portugal (Comas-Rengifo et al., 2015), is absent in La Mola, likely restricted to the nearby epioceanic crevices in the Subbetic *s.s.* (Vörös, 2002; Baeza-Carratalá et al., 2015). Also, koninckinid-beds are not recorded during this timespan in the epicontinental shelves of the Iberian Range, but are recorded in other epicontinental regions (e.g., Germany).

On the contrary, the affinity of Ass. 2b is maximum with epicontinental areas such as the Lusitanian Basin, probably due to similar environmental conditions. In this sense, the Lusitanian Basin was an epicontinental subsiding and gently-sloping ramp that was strongly influenced by tectonic activity (e.g., Alméras and Elmi, 1993; Duarte and Soares, 1993; Andrade, 2006), where sediments from shallower proximal environments to a deeper distal basin are recorded. A relatively comparable situation could have taken place on the transitional slope ramp of the La Mola region, between the trough of the Intermediate Domain and the Eastern Subbetic. This situation triggered the arrival of epicontinental taxa to the more intra-epioceanic habitats, due to the partial persistence in the transitional areas of environmental factors such as, for example, terrigenous input or nutrient availability, enabling epicontinental brachiopod settlement around the La Mola region (Fig. 6).

Thus, in the absence of Prebetic outcrops with brachiopod fauna in this easternmost part, the La Mola region can be regarded as the Lower Jurassic outcrops closest to the epicontinental habitats in the Betic Cordillera. Consequently, this region, linking the epicontinental areas to the epioceanic Subbetic ones, enabled faunal mixing and exchange between both environments, as epicontinental influences (Ass. 2b) have been detected in the transitional area of La Mola (Fig. 6), inferred from taxa regularly recorded in the epicontinental platforms from the Iberian and Lusitanian basins, interconnected with more Mediterranean Subbetic ones (Ass. 2a).

Additionally, it must be taken into account that the Intermediate Domain trough, upon whose slope La Mola was situated (Nieto et al., 1994), was not fully evolved until the latest Early Jurassic, when free connection between epicontinental/epioceanic areas in the Pliensbachian-Early Toarcian was more feasible. This made it even more likely that an area remained around La Mola that would facilitate brachiopod migration and an effective dispersal seaway or, at least, did not constitute a faunal filter-barrier for brachiopods.

5.4. Refining the biochronostratigraphical record

The well-developed Jurassic sequence from La Mola presents quite a few deposits previously dated with biostratigraphical markers mainly consisting of ammonites and calpionellids. The earliest Jurassic sediments in La Mola have been documented by previous authors as a pre-Domerian dolomitic succession (Azéma, 1977; Nieto et al., 1994; Nieto, 1997), thus providing the lowest accurate chronorecords from the Lavinianum (Portisi and Cornacaldense Subzones)-Algovianum Zones (Azéma, 1977; Iñesta, 1993; Nieto et al., 1994; Nieto, 1997). Additionally, the comprehensive stratigraphical analysis performed by Nieto (1997) revealed a stratigraphical hiatus spanning the upper Domerian and the lower Toarcian, due to the finding of *Hildoceras bifrons* (middle Toarcian, Bifrons Zone) in the basal levels of the marly sedimentation. These levels were attributed by this author to the transition between the Gavilán Fm. and Baños Fm., overlying a hardground with lower-middle Domerian ammonite fauna. Nieto (1997) also reported these deposits assigned to the Bifrons Zone overlaid by marly-marlstone beds with *Pseudogrammoceras* sp. and *Pleydellia* sp., typifying the Fallaciosum and Aalensis Zones, respectively (upper Toarcian).

The brachiopod assemblages analyzed herein enable us to refine these depositional hiatuses and to provide new data to the approximate dating of the stratigraphical record (Fig. 7). Hence, in the pre-Domerian whitish wackestone beds, biochronostratigraphical data from brachiopod Ass. 1 point to a latest Sinemurian-Eearly Pliensbachian age (Raricostatum-Aenigmaticum Zones).

Successively, Ass. 2a has been reported as presenting a wider distribution, ranging from the Demonense (lower Pliensbachian)-Polymorphum (lower Toarcian) Zones. However, the presence of distinctive uppermost Pliensbachian biomarkers in nearby basins such as *P. gignouxi* and *Cirpa* aff. *latifrons* (upper Algovianum-Emaciatum Zones) has been confirmed within this assemblage, also being recorded around the Pliensbachian-Toarcian (Pb-To) boundary, in the Elisa Subzone within the Internal Betic Zone (Baeza-Carratalá et al., 2011a). The taxa making up Ass. 2b are also representative from the Pb-To transition, spanning the Emaciatum-early Polymorphum Zones.

Likewise, Assemblage 3 is an additional marker that contributes to improve the data on the biochronostratigraphical gaps around the Pb-To boundary (Fig. 7). *Lobothyris arcta* and *Liospiriferina undulata* are the constituents of an assemblage whose distribution ranges from the uppermost Pliensbachian up to the lowermost Toarcian (Polymorphum Zone). Despite their first occurrence in the uppermost Spinatum Zone (= Algovianum of the Mediterranean Domain) and that *L. undulata* is even recorded in the basal Serpentinum Zone (Elegantulum Subzone), this assemblage mainly occurs within the Tenuicostatum (= Polymorphum) Zone.

Consequently, the biochronostratigraphical gap around the Pb-To boundary has now been calibrated to span the Serpentinum Zone and probably the uppermost Polymorphum Zone (Fig. 7). The occurrence of Ass. 3 close to the *H. bifrons*-bearing levels might also be related to a temporal averaging of the lower and middle Toarcian specimens. From the middle Toarcian onward, previous authors have recorded biostratigraphical markers from the Bifrons-Aalensis Zones, but no brachiopods have been recorded, thus preventing more accurate calibration in these sediments.

6. Conclusions

The newly collected Lower Jurassic brachiopod fauna from La Mola (Alicante province, Betic Cordillera) yielded 23 different taxa (9 rhynchonellids, 8 spiriferinids, 6 terebratulids) arranged into three major assemblages. Most of these species are documented for the first time in this area. The brachiopod biostratigraphical data allow refining and calibrating biochronostratigraphical gaps and depositional hiatuses in the pre-Domerian deposits of the Gavilán Fm. and around the Pb-To boundary, hitherto based mainly upon the scarce ammonite chronorecord. Assemblage 1 typifies the uppermost Sinemurian-lower Pliensbachian deposits (Raricostatum-Aenigmaticum Zones). Assemblage 2 (subdivided into Ass. 2a and 2b) is representative of the upper Pliensbachian-lowermost Toarcian, with index taxa of Ass. 2a (more distinctive from the Demonense-Tenuicostatum Zones) being successively replaced by those of Ass. 2b (mainly restricted to the Elisa-Mirabile Subzones). Assemblage 3 ranges from the uppermost Spinatum Zone to the Semicelatum Subzone.

The lowermost Jurassic deposits, where Assemblages 1 and 2a are recorded, closely resemble the nearby Subbetic facies. This fauna shows a mainly Mediterranean affinity, revealing a free connection with the Subbetic area at that time, but also sharing several constituents with the African and Northeastern Iberian basins. Assemblage 2b evidences high affinity with the Eastern Subbetic and the Internal Betic assemblages, but also with those of the peri-Iberian epicontinental platform system. Finally, the representative taxa of Assemblage 3 do not show affinity with the core areas of the Mediterranean province and fully coincide with the assemblages from the peri-Iberian platform system integrated in the

NW-European province, making this last assemblage a marginal assemblage of the westernmost Tethyan areas prior to the ETOAE.

The brachiopod-based paleobiogeographical analysis reveals that the environmental conditions prevailing in the La Mola region enabled a faunal mixing between the epioceanic and epicontinental environments, due to the fact that epicontinental influences are seen to be associated with the Mediterranean inhabitants of the transitional slope surrounding the La Mola area, thus triggering the arrival of epicontinental taxa in the more intra-epioceanic Subbetic habitats. Accordingly, this region contributed to brachiopod migration as an effective dispersal seaway or, at least, did not constitute an ecological filter-barrier for brachiopods in the Pliensbachian-early Toarcian timespan.

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References

Ager, D.V., 1967. Some Mesozoic Brachiopods in the Tethys region, in: Adams, C.G., Ager, D.V. (Eds.), Aspects of Tethyan Biogeography. Systematics Association Publication 7, 135–151.

Ager, D.V., 1971. Space and time in brachiopod history, in: Middlemiss, F., Rawson, P., Newall, G. (Eds.), Faunal Provinces in Space and Time. Geological Journal Special Issue 4, 95–110.

Ager, D.V., 1973. Mesozoic Brachiopoda, in: Hallam, A. (Ed.), Atlas of Palaeobiogeography. Elsevier, Amsterdam, pp. 431–436.

Ager, D.V., 1993: Mesozoic brachiopods and seamounts, in: Pálfy, J., Vörös, A. (Eds.), Mesozoic Brachiopods of Alpine Europe. Hungarian Geological Society, Budapest, pp. 11–13.

Alméras, Y., Elmi, S., 1993. Palaeogeography, physiography, palaeoenvironments and brachiopod communities. Example of the Liassic brachiopods in the Western Tethys. Palaeogeography Palaeoclimatology Palaeoecology 100, 95–108.

Alméras, Y., Fauré, P., 2000. Les Brachiopodes liasiques des Pyrénées. Paléontologie, Biostratigraphie, Paléobiogéographie et Paléoenvironnements. Strata 36, 1–395.

Alméras, Y., Fauré, P., 2007. *Lobothyris sinemuriensis* (Oppel) et faune de brachiopodes associée (Sinémurien, France). Évolution du genre *Lobothyris* Buckman (Brachiopodes, Térébratulidés). Revue de Paléobiologie Genève 26, 335–358.

Alméras, Y., Ameur, M., Elmi, S., 1993. *Prionorhynchia regia* (Rothpletz), Rhynchonellidé du Lias maghrébin et Evolution du genre *Prionorhynchia* Buckman. Bollettino della Società Paleontologica Italiana 32, 59–77.

Alméras, Y., Elmi, S., Fauré, P., 2007. Les Brachiopodes Liasiques d'Algérie Occidentale: Documents des Laboratoires de Géologie Lyon 163, 3–241.

Andrade, B., 2006. Los braquiópodos del tránsito Jurásico Inferior–Medio de la Cuenca Lusitánica (Portugal). Coloquios de Paleontología 56, 5–194.

Aurell, M., Meléndez, G., Olóriz, F., Bádenas, B., Caracuel, J., García-Ramos, J.C., Goy, A., Linares, A., Quesada, S., Robles, S., Rodríguez-Tovar, F.J., Rosales, I., Sandoval, J., Suarez de Centi, C., Tavera, J.M., Valenzuela, M., 2002. Jurassic, in: Gibbons, W., Moreno, T., (Eds.), The Geology of Spain. The Geological Society, London, pp. 213–253.

Azéma, J., 1977. Étude géologique des zones externes des Cordillères Bétiques aux confins des provinces d´Alicante et de Murcie (Espagne). Ph.D. Thesis, Université Pierre et Marie Curie, Paris, 393 p.

Baeza-Carratalá, J.F., 2011. New Early Jurassic brachiopods from the Western Tethys (Eastern Subbetic, Spain) and their systematic and paleobiogeographic affinities. Geobios 44, 345–360.

Baeza-Carratalá, J.F., 2013. Diversity patterns of Early Jurassic brachiopod assemblages from the westernmost Tethys (Eastern Subbetic). Palaeogeography Palaeoclimatology Palaeoecology 381-382, 76–91.

Baeza-Carratalá, J.F., García Joral, F., 2012. Multicostate zeillerids (Brachiopoda, Terebratulida) from the Lower Jurassic of the Eastern Subbetic (SE Spain) and their use in correlation and paleobiogeography. Geologica Acta 10, 1–12.

Baeza-Carratalá, J.F., Sepehriannasab, B., 2014. Early Jurassic (latest Toarcian) brachiopods from the northeastern margin of the Western Tethys (Central Iran) and their paleobiogeographical significance. Geobios 47, 3–17.

Baeza-Carratalá, J.F., García Joral, F., Tent-Manclús, J.E., 2011a. Biostratigraphy and palaeobiogeographic affinities of the Jurassic brachiopod assemblages from Sierra Espuña

(Maláguide Complex, Internal Betic Zones, Spain). Journal of Iberian Geology 37, 137–151.

Baeza-Carratalá, J.F., Vörös, A., Dulai, A., Tent-Manclús, J.E., 2011b. Brachiopod assemblages from the Early–Middle Jurassic transition in the Eastern Subbetic (SE Spain): Systematic and palaeobiogeographic implications and palaeoenvironmental significance. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 262, 171–197.

Baeza-Carratalá, J.F., García Joral, F., Sandoval, J., 2014. Bajocian-Early Bathonian (Jurassic) brachiopods from the Subbetic domain (Betic Cordillera, SE Spain): Taxonomy and palaeobiogeographic implications. Neues Jahrbuch für Geologie und Palaontologie, Abhandlungen 274, 1–24.

Baeza-Carratalá, J.F., García Joral, F., Giannetti, A., Tent-Manclús, J.E., 2015. Evolution of the last koninckinids (Athyridida, Koninckinidae), a precursor signal of the Early Toarcian mass extinction event in the Western Tethys. Palaeogeography Palaeoclimatology Palaeoecology 429, 41–56.

Bassoullet, J.P., Elmi, S., Poisson, A., Ricou, L.E., Cecca, F., Bellión, Y., Giraud, R., Baudin, F., 1993. Middle Toarcian (184–182 Ma.), in: Dercourt, J., Ricou, L.E., Vrielynck, B. (Eds.), Atlas of Tethys Palaeoenvironmental Maps. Beicip-Franlab, Rueil-Malmaison.

Caracuel, J.E., Fernández-López, S.R., Tent-Manclús, J.E., Yébenes, A., 2004. Itinerario paleontológico por el Cerro de La Cruz (Sierra del Reclot), in: Alfaro, P., Andreu, J.M., Estévez, A., Tent-Manclús, J.E., Yébenes, A. (Eds.), Geología de Alicante, pp. 245–260.

Cariou, E., Hantzpergue, P., 1997. Groupe Français d'Études du Jurassique, biostratigraphie du Jurassique ouest-européen et méditerranéen. Zonations parallèles et distribution des invertébrés et microfossiles. Bulletin des Centres de Recherches Exploration-Production d'Elf-Aquitaine 17, 1–400.

Colás, J., García Joral, F., 2012. Morphology and environment in the Jurassic Nucleatidae (Brachiopoda) from Western Tethys. Lethaia 45, 178–190.

Comas-Rengifo, M.J., 1982. El Pliensbachiense de la Cordillera Ibérica. Ph.D. Thesis, Universidad Complutense Madrid., 591 p. (unpublished).

Comas-Rengifo, M.J., García-Joral, F., Goy, A., 2006. Spiriferinida (Brachiopoda) del Jurásico Inferior del NE y N de España: distribución y extinción durante el evento anóxico oceánico del Toarciense inferior. Boletín de la Real Sociedad Española de Historia Natural, Sección Geológica 101, 147–157.

Comas-Rengifo, M.J., Duarte, L.V., García Joral, F., Goy, A., 2013. Los braquiópodos del Toarciense Inferior (Jurásico) en el área de Rabaçal-Condeixa (Portugal): distribución estratigráfica y paleobiogeografía. Comunicações Geológicas 100, 37–42.

Comas-Rengifo, M.J., Duarte, L.V., Félix, F.F., García Joral, F., Goy, A., Rocha, R.B., 2015. Latest Pliensbachian–Early Toarcian brachiopod assemblages from the Peniche section (Portugal) and their correlation. Episodes 38, 2–8.

Davidson, T., 1851. A Monograph of the British Fossil Brachiopoda (Vol. 1, Part 3: The Oolitic and Liasic Brachiopoda). Palaeontographical Society (London) Monograph 4, 1–64.

De Ruig, M.J., 1992. Tectono-sedimentary evolution of the Prebetic fold belt of Alicante (SE Spain). A study of stress fluctuations and foreland basin deformation. Drukkerij Elinkwijk, Utrecht, 207 p.

Duarte, L.V., Soares, A.F., 1993. Eventos de natureza tempestítica e turbidítica no toarciano inferior da Bacia Lusitaniana (sector norte). Cadernos de Geografía 12, 89–95.

Elmi, S., Marok, A., Sebane, A., Alméras, Y., 2006. Importance of the Mellala section (Traras Mountains, NW Algeria) for the correlations of the Pliensbachian/Toarcian boundary. Volumina Jurassica 4, 158–160.

Fallot, P., 1945. Estudios geológicos en la Zona Subbética entre Alicante y el río Guadiana Menor. Monografías del Consejo Superior de Investigaciones Científicas, Instituto Lucas Mallada 5, 1–719.

Gahr, M., 2005. Response of Lower Toarcian (Lower Jurassic) macrobenthos of the Iberian Peninsula to sea level changes and mass extinction. Journal of Iberian Geology 31, 197–215.

García Joral, F., Goy, A., 2000. Stratigraphic distribution of Toarcian brachiopods from the Iberian Range and its relation to depositional sequences. Georesearch Forum 6, 381–386.

García Joral, F., Gómez, J.J., Goy, A., 2011. Mass extinction and recovery of the Early Toarcian (Early Jurassic) brachiopods linked to climate change in northern and central Spain. Palaeogeography Palaeoclimatology Palaeoecology 302, 367–380.

García-Hernández, M., López-Garrido, A.C., Rivas, P., Sanz de Galdeano, C., Vera, J.A., 1980. Mesozoic paleogeographic evolution of the External Zone of the Betic Cordilleras. Geologie en Mijnbouw 59, 155–168.

Goy, A., Comas-Rengifo, M.J., Arias, C., García Joral, F., Gómez, J.J., Herrero, C., Martínez, G., Rodrigo, A., 1997. El Tránsito Pliensbachiense/Toarciense en el sector central de la

Rama Aragonesa de la Cordillera Ibérica (España). Cahiers de l'Université Catholique de Lyon 10, 159–179.

Hallam, A., 1971. Provinciality in Jurassic faunas in relation to facies and palaeogeography, in: Middlemiss, F.A., Rawson, P.F., Newall, G. (Eds.), Faunal Provinces in Space and Time. Geological Journal Special Issue 4, 129–152.

Iñesta, M., 1993. El Jurásico del Cerro de la Mola y su fauna de braquiópodos. Revista Cidaris 2(3), 4–19.

Iñesta, M., Szabó, J., Szente, I., 1990. A Pliensbachian gastropod and bivalve faunula from the la Mola Hill (Betic Cordilleras, Spain). Annales historico-naturalis Musei nationalis hungarici 82, 19–23.

Jiménez de Cisneros, D., 1920. Noticia acerca del encuentro de numerosos yacimientos del Liásico medio alpino en el SE de España. Boletín de la Real Sociedad Española de Historia Natural 20, 226–236.

Jiménez de Cisneros, D., 1927. El Lías alpino medio del SE de España. Compte-Rendu 14ème Congrès Géologique International, Madrid, pp. 3-14.

Kaesler, R.L., Selden, P.A. (Eds.), 1997–2007. Treatise on Invertebrate Paleontology. Part H, Brachiopoda, Revised, Vols. 1–6. Geological Society of America and Paleontological Institute, Boulder, Colorado and Lawrence, Kansas.

Manceñido, M.O., 2002. Paleobiogeography of Mesozoic brachiopod faunas from Andean–Patagonian areas in a global context. Geobios Spec. Mem. 24, 176–192.

Martín-Algarra, A., Ruiz-Ortiz, P.A., Vera, J.A., 1992. Factors controlling Cretaceous turbidite deposition in the Betic Cordillera. Revista de la Sociedad Geológica de España 5, 53–80.

Molina, J.M., Ruiz-Ortiz, P.A., Vera, J.A., 1999. A review of polyphase karstification in extensional tectonic regimes: Jurassic and Cretaceous examples, Betic Cordillera, southern Spain. Sedimentary Geology 129, 71–84.

Nieto, L.M., 1997. La cuenca subbética mesozoica en el sector oriental de las Cordilleras Béticas. Ph.D. Thesis. Universidad Granada, 562 p.

Nieto, L.M., Molina, J.M., Ruiz-Ortiz, P.A., 1994. El talud submarino de transición entre el Dominio Intermedio y el Subbético Externo durante el Jurásico (La Mola de Novelda, prov. de Alicante). Geogaceta 16, 70–73.

Nieto, L.M., Rodríguez-Tovar, F.J., Molina, J.M., Reolid, M., Ruiz-Ortiz, P.A., 2014. Unconformity surfaces in pelagic carbonate environments: a case from the Middle

Bathonian of the Betic Cordillera, SE Spain. Annales Societatis Geologorum Poloniae 84, 281–295.

Olóriz, F., Caracuel, J.E., Ruiz-Heras, J.J., Rodríguez-Tovar, F.J., Marques, B., 1996. Ecostratigraphic approaches, sequence stratigraphy proposals and block tectonics: examples from epioceanic swell areas in south and east Iberia. Palaeogeography Palaeoclimatology Palaeoecology 121, 273–295.

Seguenza, G., 1885. Le Spiriferina dei vari Piani del Lias messinese. Boletino della Società Geologica Italiana 4, 377–497.

Tomasových, A., 2006. A new Early Jurassic Rhynchonellid Brachiopod from the western Tethys and implications for systematics of Rhynchonellids from the Triassic-Jurassic Boundary. Journal of Paleontology 80, 212–228.

Vera, J.A., 1988. Evolución de los sistemas de depósito en el margen ibérico de la Cordillera Bética. Revista de la Sociedad Geológica de España 1, 373–391.

Vera, J.A., 1998. El Jurásico de la Cordillera Bética: Estado actual de conocimientos y problemas pendientes. Cuadernos de Geología Ibérica 24, 17–42.

Vera, J.A., 2001. Evolution of the South Iberian Continental Margin. Mémoires du Muséum National d'Histoire Naturel de Paris 186, 109–143.

Vera, J.A., Martín-Algarra, A., Sánchez-Gómez, M., Fornós, J.J., Gelabert, B., 2004. Cordillera Bética y Baleares, in: Vera, J.A. (Ed.), Geología de España. SGE-IGME, pp. 345–464.

Vörös, A., 1984. Lower and Middle Jurassic brachiopod provinces in the western Tethys. Annales Universitatis Scientiarum Budapestinensis de Rolando Eötvös nominatae, Sectio Geologica 24, 207–233.

Vörös, A., 1986. Brachiopod palaeocology on a Tethyan Jurassic seamount (Pliensbachian, Bakony Mountains, Hungary). Palaeogeography Palaeoclimatology Palaeoecology 57, 241–271.

Vörös, A., 1993. Jurassic microplate movements and brachiopod migrations in the western part of the Tethys. Palaeogeography Palaeoclimatology Palaeoecology 100, 125–145.

Vörös, A., 2002. Victims of the Early Toarcian anoxic event: the radiation and extinction of Jurassic Koninckinidae (Brachiopoda). Lethaia 35, 345–357.

Vörös, A., 2005. The smooth brachiopods of the Mediterranean Jurassic: refugees or invaders? Palaeogeography Palaeoclimatology Palaeoecology 223, 222–242.

Vörös, A., 2009. The Pliensbachian brachiopods of the Bakony Mountains (Hungary). Geologica Hungarica, series Paleontologica 58, 1–300.

Vörös, A., Dulai, A., 2007. Jurassic brachiopods of the Transdanubian Range (Hungary); stratigraphical distribution and diversity changes. Fragmenta Palaeontologica Hungarica 24–25, 51–68.

Table and Figure captions.

Table 1. Presence of Lower Jurassic brachiopod taxa in assemblages 1-3 from the La Mola region (X) and occurrence of these taxa in various representative epicontinental/epioceanic environments (x), especially from the peri-Iberian platform system and nearby basins (see text for data sources). Species shared with La Mola assemblages are given in total number (NT: number of taxa) and percentages (within parentheses).

Fig. 1. **A**. Geographical situation of the study area in Southeastern Spain. **B**. Situation of the La Mola outcrop within the context of the Eastern Betic Cordillera in the Alicante Province.

Fig. 2. **A**. General view of the southern side of La Mola Hill, where the Lower Jurassic stratigraphical section contains the most complete and fossil-rich succession. 1: Massive dolomites overlaid by massive wackestone beds upwards; 2: Red crinoidal limestone beds; 3: Yellowish marl alternating with pseudonodular limestone levels; 4: Well-bedded whitish limestone beds. **B**. Massive bioclastic wackestone-packstone beds with some oncolites and brachiopod shells. **C**. Stratigraphical contact between massive limestone beds (below) and yellowish micritic limestone and marlstone beds (to the top) marked by an unconformity surface associated with a greenish-grayish marly level. In this part of the section, the red crinoidal limestone unit is missing. **D**. Unconformity surface with brachiopods, ammonites, gastropods, belemnites and Fe-Mn oxides included in the red crinoidal limestone unit. **E**. Lower Toarcian yellowish alternating marl-pseudonodular limestone beds.

Fig. 3. Synthetic Lower Jurassic lithostratigraphical sketch showing brachiopod occurrences and the successive biostratigraphical distribution and replacement of assemblages in the La Mola region. **1**. Massive dolostone sequence. **2**. Whitish-creamy wackestone beds. **3**. Red crinoidal limestone beds. **4**. Hardground surface with Fe-Mn crusts. **5**. Yellowish marls alternating with pseudonodular marly limestone levels. **6**. Highly bioturbated reddish marly limestone level. **7**. Well-bedded whitish micritic limestone succession.

Fig. 4. Some representative species of La Mola brachiopod assemblages. **1-7.** Assemblage 2a, early?-late Pliensbachian. 1: *Cirpa briseis* (Gemmellaro), specimen LM.Cb1; 2: *Quadratirhynchia crassimedia* (Buckman), specimen LM.Q.2; 3: *Liospiriferina alpina*

(Oppel), specimen LM.La.1; 4: *Linguithyris aspasia* (Zittel), specimen LM.Lia.1; 5: *Cisnerospira angulata* (Oppel), specimen LM.Ca.1; 6: *Prionorhynchia gignouxi* (Jiménez de Cisneros), specimen LM.Pg.1; 7: *Cirpa* aff. *latifrons* (Zieten), specimen LM.Cl. **8-11**. Assemblage 2b, late Pliensbachian. 8: *Lobothyris* cf. *edwardsi* (Davidson), specimen LM.Le.1; 9-11: *Lobothyris* sp. 1, specimens LM.Lc.1, LM.Lc.2, and LM.Lc.3, respectively. **12-15**. Assemblage 3, latest Pliensbachian-Early Toarcian. 12, 13: *Liospiriferina undulata* (Seguenza), specimens LM.Lu.1 and LM.Lu.2, respectively; 14, 15: *Lobothyris* cf. *arcta* (Dubar), specimens LM.Loa.1 and LM.Loa.2, respectively. **16, 17**. Assemblage 1, Sinemurian-Pliensbachian transition. 16: *Dispiriferina*? *segregata* (Di Stefano), specimen LM.Ds.1; 17: Hand sample of the bioclastic wackestone beds containing *Calcirhynchia plicatissima* (Quenstedt) (white arrow) and *Gibbirhynchia curviceps* (Quenstedt) (black arrow). All specimens were coated with magnesium oxide. For all specimens, a = dorsal view, b = anterior view, c = lateral view, d = ventral view except for specimen 5 = posterior view. Scale bars: 1 cm.

Fig. 5. Distribution of representative taxa of Assemblages 2b (**A**) and 3 (**B**) in the Western Tethys. E = *Lobothyris edwardsi* and closely related forms; T = *Lobothyris* sp. 1; black triangle = *Lobothyris arcta*; black spot = *Liospiriferina*? *undulata.* Early Jurassic paleomap slightly modified after Bassoullet et al. (1993). See text for data sources.

Fig. 6. **A**. Distribution of Assemblage 2 through the Early Jurassic peri-Iberian platform system, showing preferential affinities of their constituent sub-assemblages. Paleomap redrawn and slightly modified after Vera (1998). 1: Iberian Range; 2: Prebetic Zone; 3: Lusitanian Basin; 4: Intermediate Domain; 5: Subbetic Zone; 6: Internal Betic Zones; 7: Pyrenees; black square: La Mola situation; arrows show the spreading inferred and possible migration routes. **B**. Schematic model of the Jurassic South Iberian paleomargin (modified after Olóriz et al., 1996) showing the inferred transitional condition of the La Mola region in the distribution of epioceanic (2a) and epicontinental (2b) taxa, likely influenced by several environmental factors. The vertical scale of the sea bottom physiography was magnified for a better visualization of the epicontinental/epioceanic distinction.

Fig. 7. Combination of biochronological ammonite data reported by previous authors (see text for data sources) with those provided by brachiopod assemblages from La Mola section,

together enabling the calibration of some hiatuses in the Lower Jurassic biochronostratigraphical record.

Table 1.

	Assemblages					**Representative epicontinental/epioceanic environments**						
La Mola	1	2	2a	2b	3	Eastern Subbetic	Internal Betic Zone	Iberian Range	Lusitanian Basin	Bakony	West. Algeria	Pyrenees
Prionorhynchia regia	X					x					x	
Calcirhynchia plicatissima	X					x						
Gibbirhynchia curviceps	X					x	x	x	x	x	x	x
Cisnerospira aff. *adscendens*	X					x	x					
Dispiriferina? *segregata*	X					x				x		
Quadratirhynchia crassimedia	X	X	X	X		x	x				x	x
Liospiriferina alpina	X	X	X	X		x	x	x		x	x	x
Linguithyris aspasia		X	X			x				x	x	
Cirpa briseis		X	X			x					x	x
Prionorhynchia cf. *flabellum*		X	X			x				x		
Prionorhynchia gignouxi		X	X			x	x					
Cisnerospira angulata		X	X			x	x	x		x	x	x
Liospiriferina obtusa		X	X			x				x		
Cirpa aff. *latifrons*		X	X			x						
Liospiriferina rostrata		X	X	X	X	x	x	x	x		x	x
Lobothyris cf. *edwardsi*		X		X				x	x			
Lobothyris sp.1		X		X					x			
Lobothyris cf. *arcta*					X	x		x	x		x	x
Liospiriferina undulata					X	x		x	x			
Assemblage 1 (NT=7)						7 (100%)	4 (57.1%)	2 (28.6%)	1 (14.2%)	3 (42.8%)	3 (42.8%)	3 (42.8%)
Assemblage 2 (NT=12)						10 (83.3%)	5 (41.7%)	4 (33.3%)	3 (25%)	5 (41.7%)	6 (50%)	5 (41.7%)
Assemblage. 2a (NT=10)						10 (100%)	5 (50%)	3 (30%)	1 (10%)	5 (50%)	6 (60%)	5 (50%)
Assemblage 2b (NT=5)						3 (60%)	3 (60%)	3 (60%)	3 (60%)	1 (20%)	3 (60%)	3 (60%)
Assemblage 3 (NT=3)						3 (100%)	1 (33.3%)	3 (100%)	3 (100%)	0 (0)%	2 (66.6%)	2 (66.6%)

Figure 1

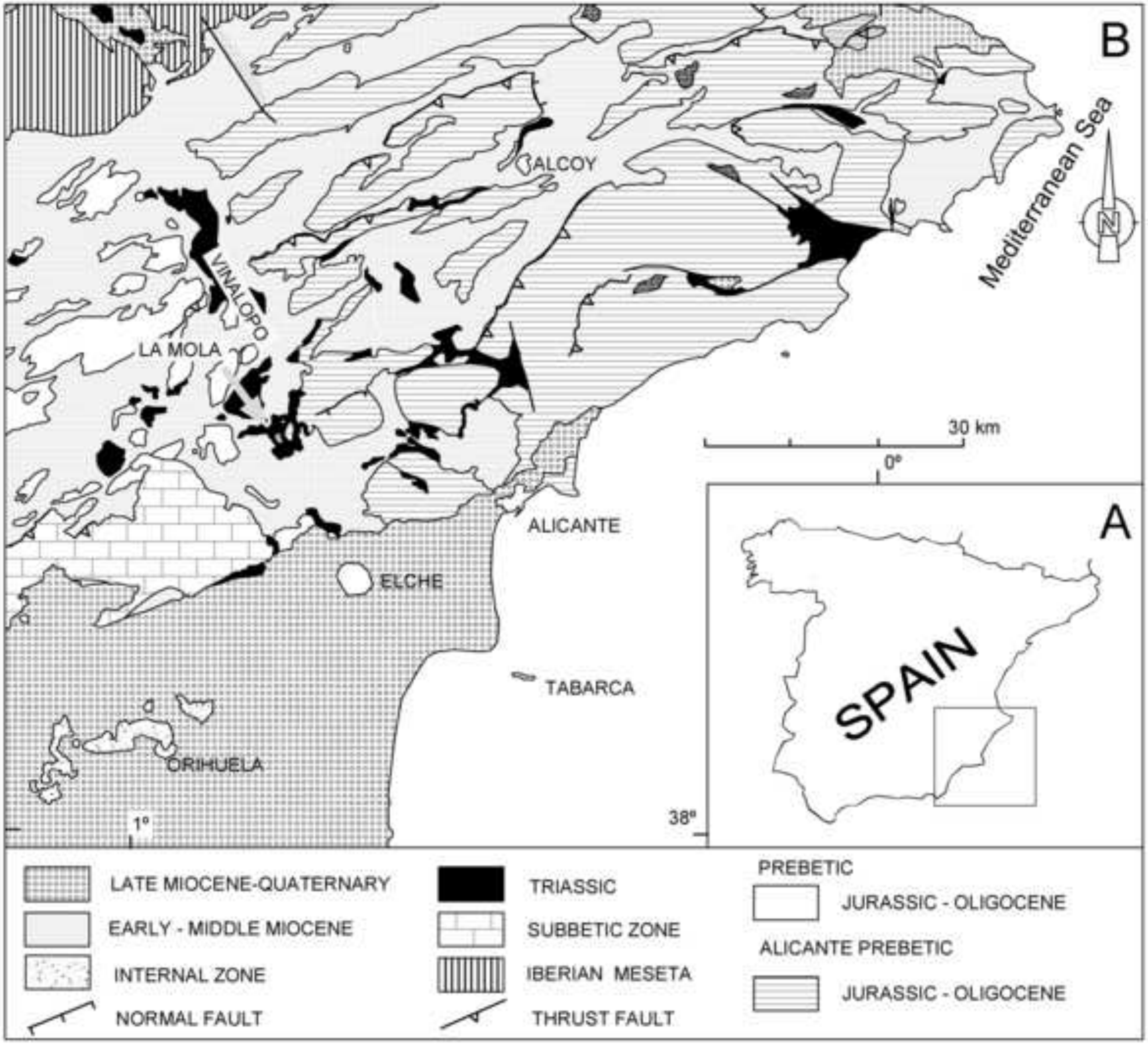

B
ALCOY
VINALOPO
LA MOLA
ALICANTE
ELCHE
TABARCA
ORIHUELA
Mediterranean Sea
N
30 km
0°
1°
38°
A
SPAIN
LATE MIOCENE-QUATERNARY
EARLY - MIDDLE MIOCENE
INTERNAL ZONE
NORMAL FAULT
TRIASSIC
SUBBETIC ZONE
IBERIAN MESETA
THRUST FAULT
PREBETIC
JURASSIC - OLIGOCENE
ALICANTE PREBETIC
JURASSIC - OLIGOCENE

Figure 2

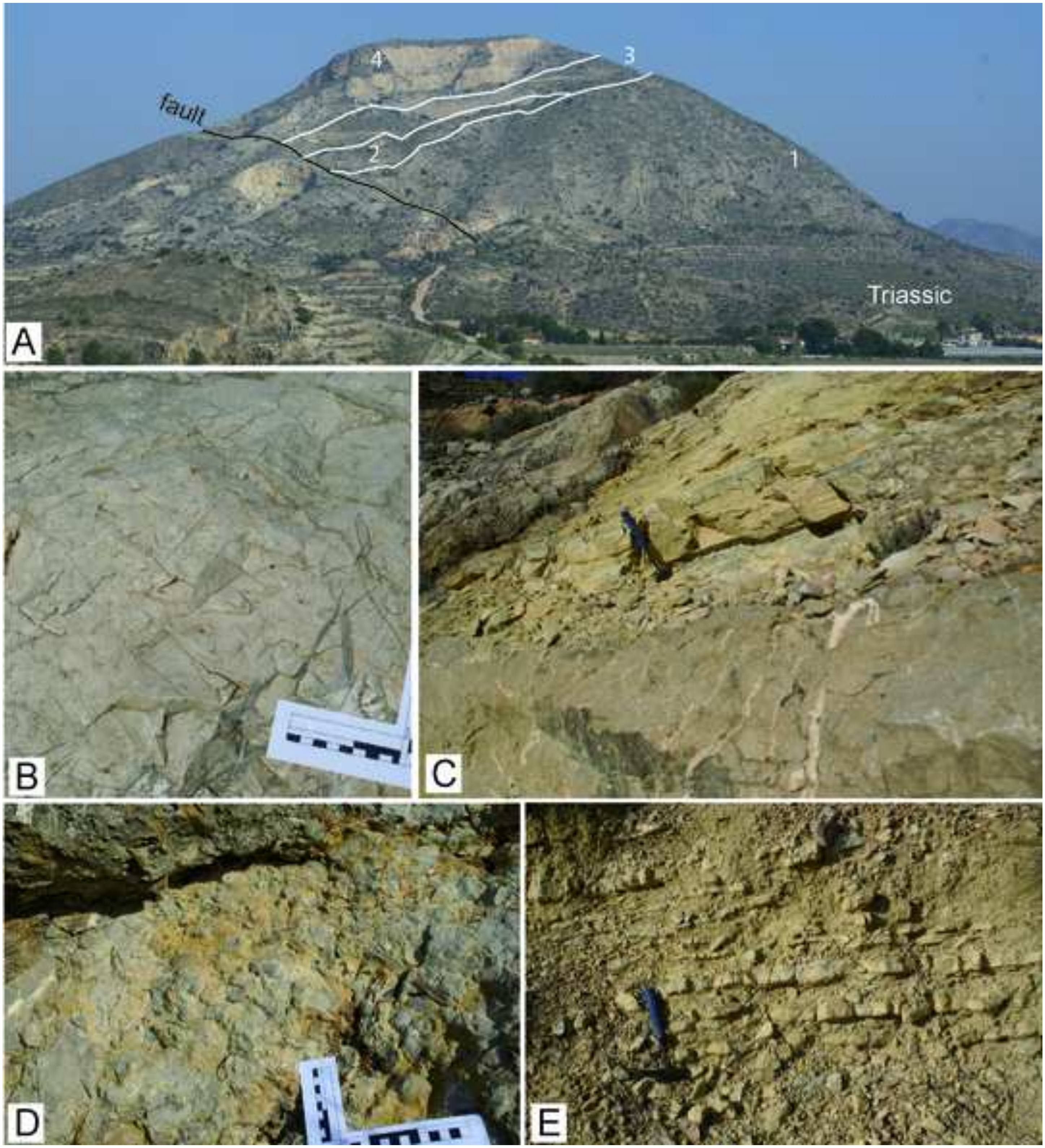
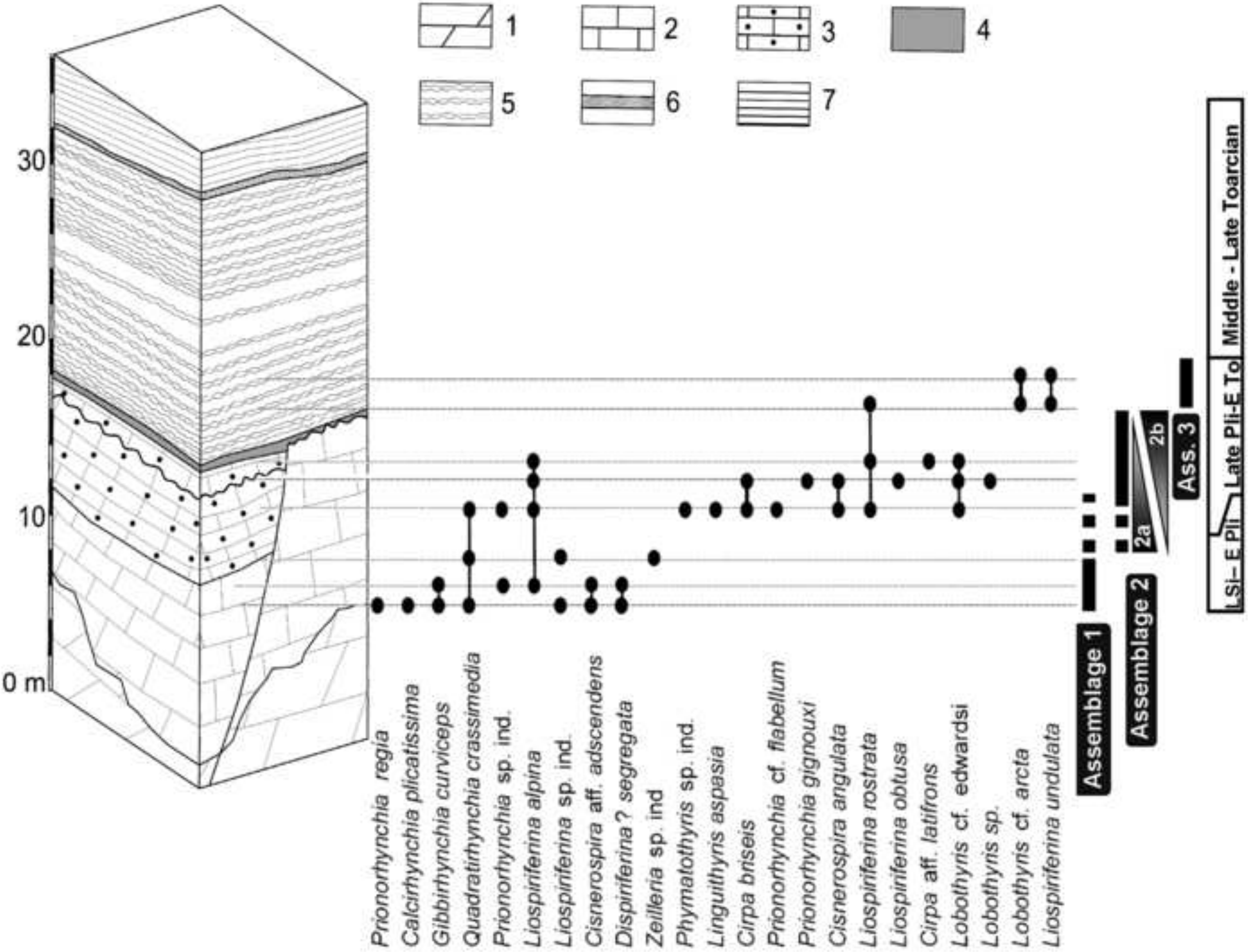
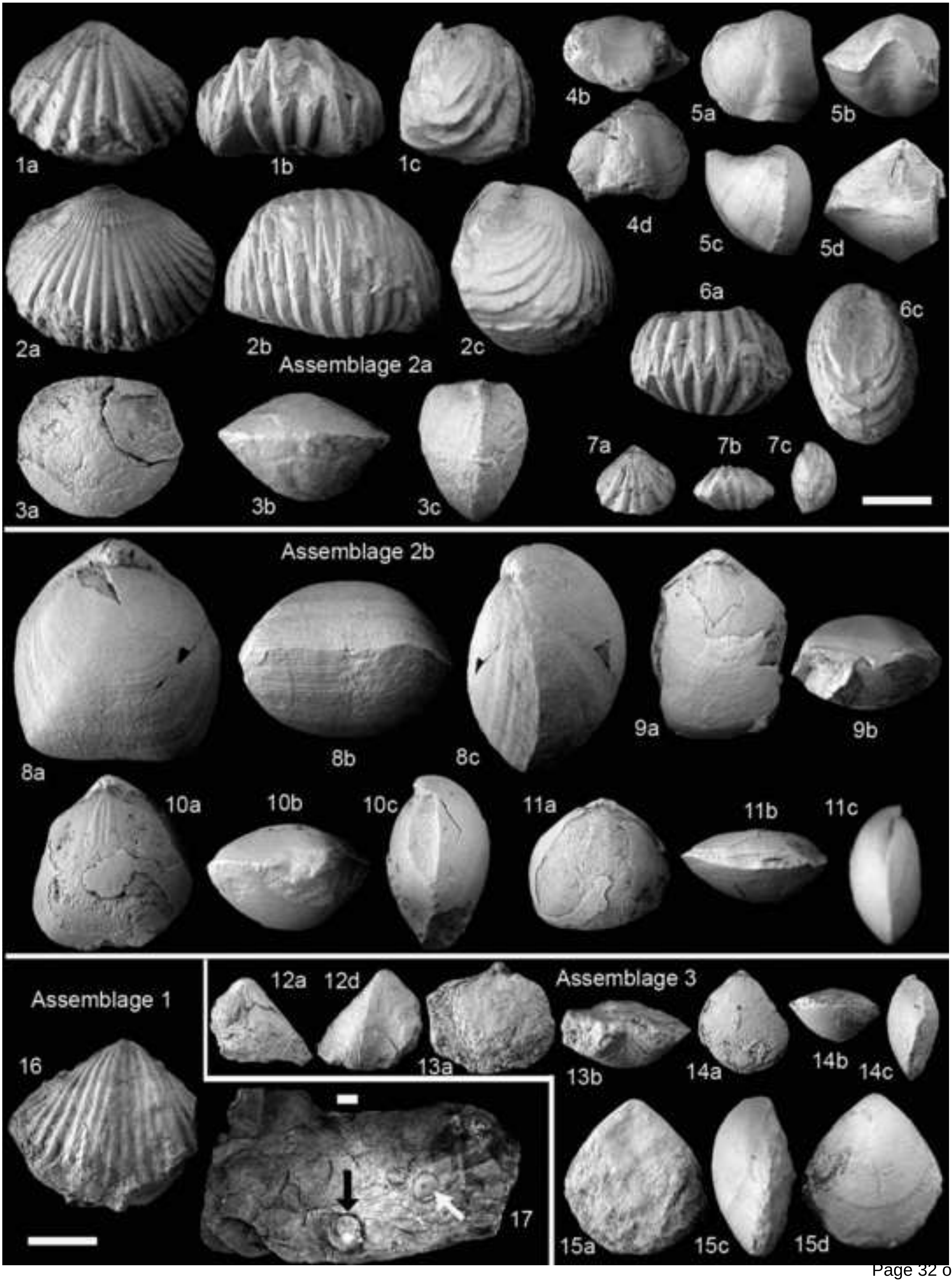


Figure 3



1
2
3
4
5
6
7
30
20
10
0 m
Prionorhynchia regia
Calcirhynchia plicatissima
Gibbirhynchia curviceps
Quadratirhynchia crassimedia
Prionorhynchia sp. ind.
Liospiriferina alpina
Liospiriferina sp. ind.
Cisnerospira aff. adscendens
Dispiriferina? segregata
Zeilleria sp. ind
Phymatothyris sp. ind.
Linguithyris aspasia
Cirpa briseis
Prionorhynchia cf. flabellum
Prionorhynchia gignouxi
Cisnerospira angulata
Liospiriferina rostrata
Liospiriferina obtusa
Cirpa aff. latifrons
Lobothyris cf. edwardsi
Lobothyris sp.
Lobothyris cf. arcta
Liospiriferina undulata
Assemblage 1
Assemblage 2
2a
2b
Ass. 3
LSi– E Pli
Late Pli-E To
Middle - Late Toarcian

Figure 4


1a
1b
1c
4b
5a
5b
4d
5c
5d
2a
2b
2c
6a
6c
Assemblage 2a
3a
3b
3c
7a
7b
7c
Assemblage 2b
8a
8b
8c
9a
9b
10a
10b
10c
11a
11b
11c
Assemblage 1
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12d
13a
Assemblage 3
13b
14a
14b
14c
16
17
15a
15c
15d

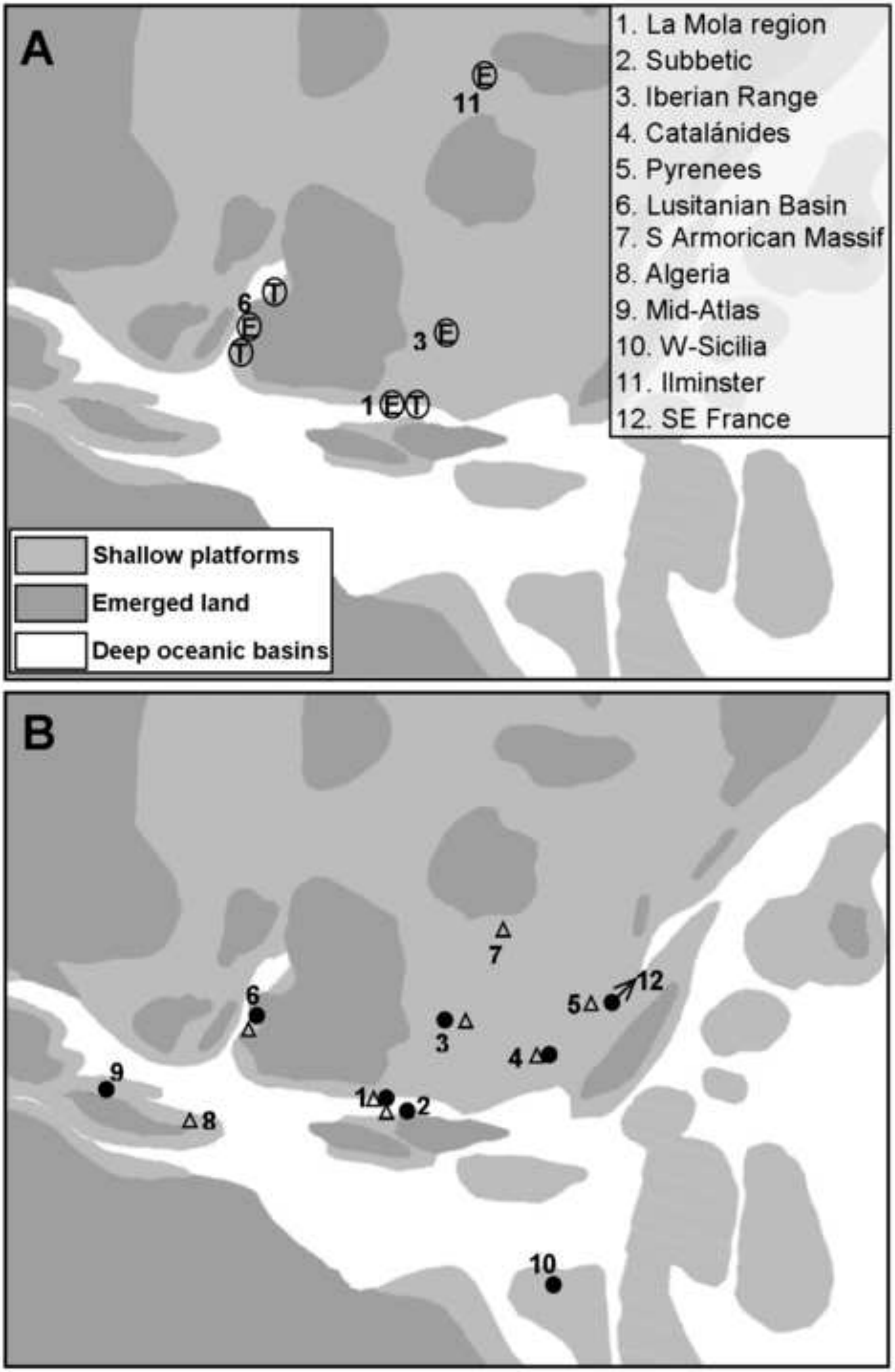

A
1. La Mola region
2. Subbetic
3. Iberian Range
4. Catalánides
5. Pyrenees
6. Lusitanian Basin
7. S Armorican Massif
8. Algeria
9. Mid-Atlas
10. W-Sicilia
11. Ilminster
12. SE France
11
E
6
T
E
T
3
E
1
E
T
Shallow platforms
Emerged land
Deep oceanic basins
B
7
6
3
4
5
12
9
8
1
2
10

Figure 6

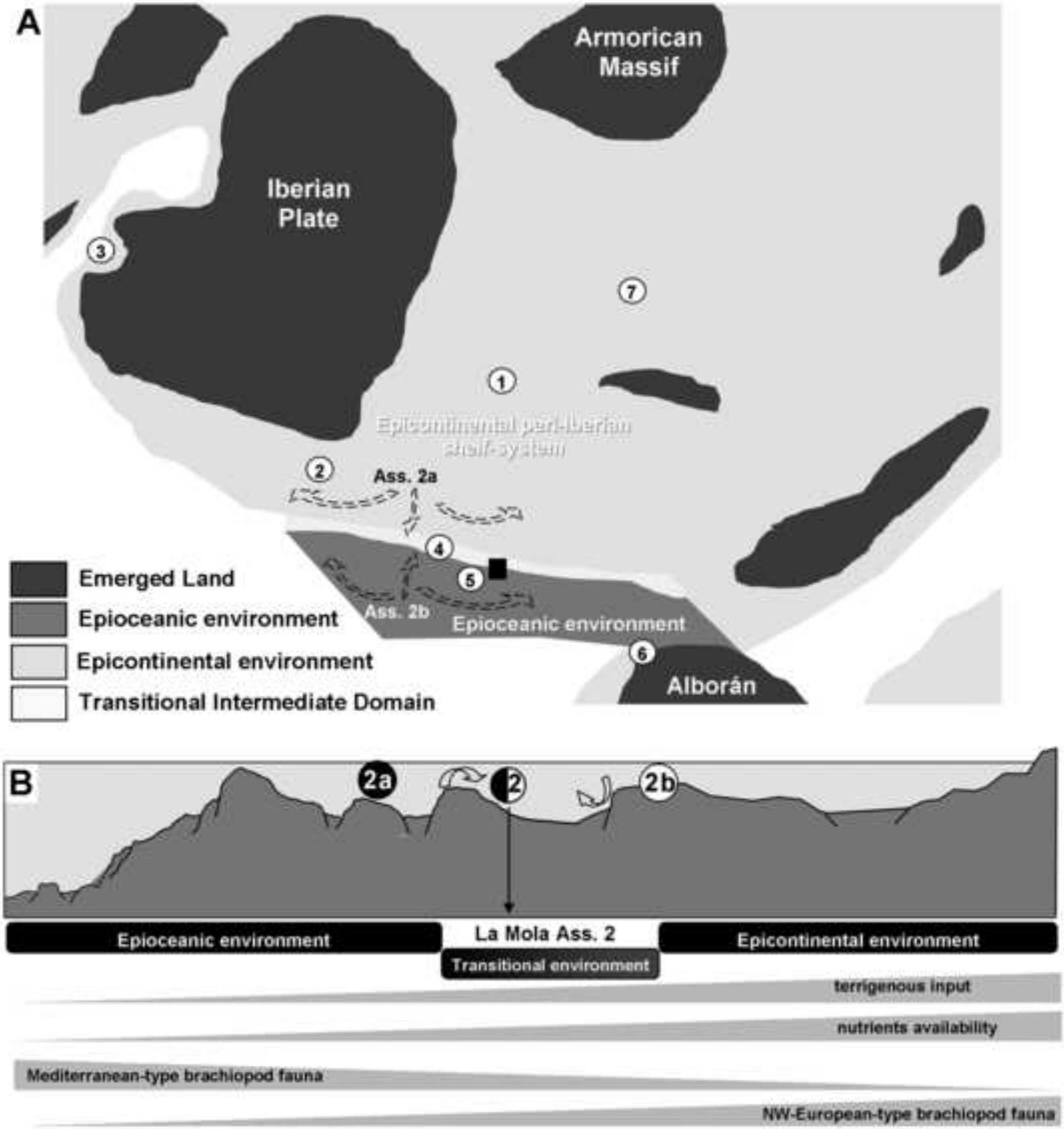
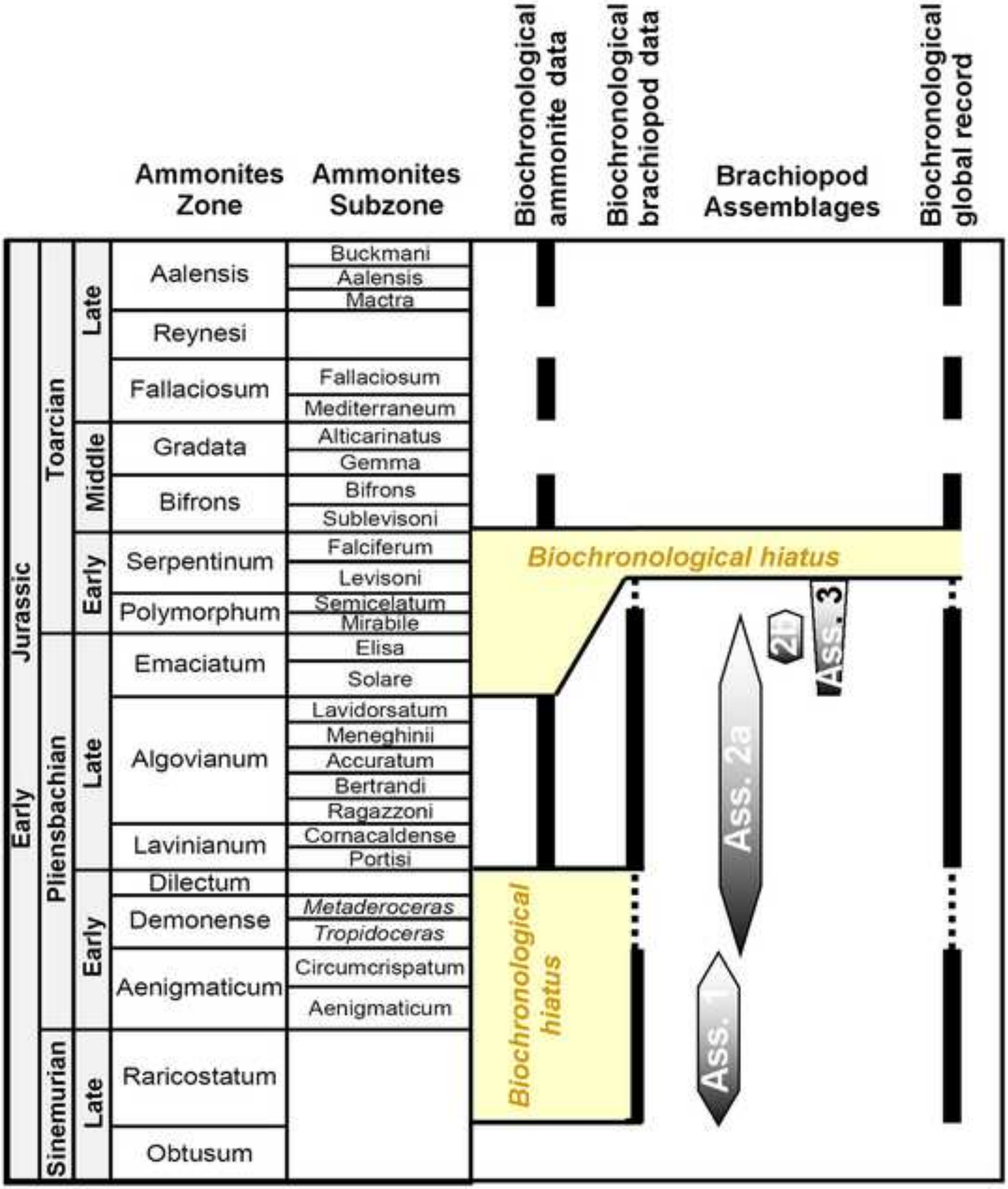

A
Armorican Massif
Iberian Plate
③
⑦
①
Epicontinental peri-Iberian shelf-system
②
Ass. 2a
④
⑤
Ass. 2b
Epioceanic environment
⑥
Alborán
Emerged Land
Epioceanic environment
Epicontinental environment
Transitional Intermediate Domain
B
2a
2
2b
Epioceanic environment
La Mola Ass. 2
Transitional environment
Epicontinental environment
terrigenous input
nutrients availability
Mediterranean-type brachiopod fauna
NW-European-type brachiopod fauna

Figure 7


Ammonites Zone
Ammonites Subzone
Biochronological ammonite data
Biochronological brachiopod data
Brachiopod Assemblages
Biochronological global record
Early Jurassic
Toarcian
Pliensbachian
Sinemurian
Late
Middle
Early
Late
Early
Late
Aalensis
Reynesi
Fallaciosum
Gradata
Bifrons
Serpentinum
Polymorphum
Emaciatum
Algovianum
Lavinianum
Dilectum
Demonense
Aenigmaticum
Raricostatum
Obtusum
Buckmani
Aalensis
Mactra
Fallaciosum
Mediterraneum
Alticarinatus
Gemma
Bifrons
Sublevisoni
Falciferum
Levisoni
Semicelatum
Mirabile
Elisa
Solare
Lavidorsatum
Meneghinii
Accuratum
Bertrandi
Ragazzoni
Cornacaldense
Portisi
Metaderoceras
Tropidoceras
Circumcrispatum
Aenigmaticum
Biochronological hiatus
Biochronological hiatus
Ass. 3
2b
Ass. 2a
Ass. 1