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First evidence of brachiopod diversification after the end-Triassic extinction from the pre-Pliensbachian Internal Subbetic platform (South-Iberian Paleomargin) ✡

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Abstract

Lower Jurassic brachiopods are widely known in the External Betic Zone. Their occurrence was so far virtually restricted to the easternmost Subbetic Zone where they underwent a diversity burst and radiation event during the late Sinemurian–early Pliensbachian interval, leading to a bloom in brachiopod diversity from the early Pliensbachian onwards. Taxonomical and paleobiogeographical analyses performed in a newly recorded assemblage from the most offshore areas of the Subbetic Basin (Granada province, Spain) reveals that this diversification event occurred earlier than expected hitherto, probably in the Turneri–Obtusum chronozones, as similarly observed in the most intra-Tethyan basins such as the Northern Calcareous Alps and Transdanubian Ranges, illustrating the recovery of the background conditions for the establishment of diversified brachiopod communities after the end-Triassic extinction event. A new rhynchonellide species, *Alebusirhynchia vorosi* nov. sp., is formally described among the ten different taxa recorded for the first time in this

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area. The Mediterranean paleobiogeographical affinities revealed by the brachiopod assemblage emphasizes that the onset of the Mediterranean/Euro-Boreal bioprovinciality and the initial brachiopod diversification in the pre-Pliensbachian Internal Subbetic platform took place earlier in the Sinemurian as well, following the Euro-Boreal monotypic record previously reported in this region.

Keywords:

Brachiopoda

Alebusirhynchia vorosi nov. sp.

Systematics

Early Jurassic radiation

Paleobiogeography

Mediterranean bioprovince

Internal Subbetic

1. Introduction

The critical end-Triassic extinction event triggered substantial changes in the benthic communities, particularly in brachiopod assemblages (Sandy, 1995; Hallam, 1996, 2002; Dulai, 2001, 2003; Tomašových and Siblík, 2007; Vörös et al., 2016). Diverse brachiopod clades were severely affected by the end-Triassic mass extinction and subsequent brachiopod records are very scarce in the lowermost Jurassic sediments (Dulai, 2001; Tomašových, 2006). In the last decades, new results suggested that post-extinction recovery of the background conditions for the establishment of diversified brachiopod communities occurred in the Western Tethys earlier in the Jurassic than originally expected. The well-documented late Sinemurian brachiopod diversity burst (Vörös, 1993; Dulai, 2003; Ruban, 2004; Vörös and Dulai, 2007; Baeza-Carratalá, 2013) was actually preceded by an early and progressive diversification that has been noticed in a few Tethyan and NW-European platforms as early as in the Hettangian-early Sinemurian times (Rossi-Ronchetti and Brena, 1953; Gaetani, 1970; Alméras and Hanzo, 1991; Dulai, 1993, 2001, 2003; Siblík, 1999; Böhm et al., 1999; Tomašových, 2006, among others).

In the Betic Ranges, the burst in brachiopod diversity is widely documented from the early Pliensbachian onwards in the easternmost External Subbetic Zone (Jiménez de Cisneros,

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1923, 1935; Baeza-Carratalá, 2011, 2013; Baeza-Carratalá et al., 2015, 2016). So far, it was understood that this peak of diversity started with a remarkable speciation and radiation episode in the latest Sinemurian-earliest Pliensbachian (Baeza-Carratalá and García Joral, 2012; Baeza-Carratalá, 2013). Nevertheless, the present paper provides evidence that the onset of this radiation in the Subbetic Basin actually started earlier than the latest Sinemurian. A new brachiopod fauna which thrived in the Internal Subbetic Zone (Venta Quesada section) reveals that this diversification event occurred a little earlier into the Sinemurian in the most offshore areas of the Subbetic Basin, as similarly observed in some other intra-Tethyan basins such as the Northern Calcareous Alps (Austria) and Transdanubian Ranges (Hungary). This diversification was probably related with an incipient pre-rifting stage of the westernmost Tethyan platform system (Vera, 1988, 1998; Molina et al., 1999), interpreted as the first Sinemurian tectonic pulses (Nieto, 1997; cf. Ruiz-Ortiz et al., 2004; Tent-Manclús, 2006), thus diversifying the ecological niches and facilitating the establishment of stable brachiopod communities. Prior to this episode, brachiopods were only occasionally reported in the Internal Subbetic deposits through a few earliest Sinemurian specimens arranged within the genus *Calcirhynchia* (Pérez-López et al., 1993).

Accordingly, taxonomical and paleobiogeographical analyses of the new brachiopod assemblage are performed, formally establishing a new rhynchonellide species based on a detailed description of its external and internal structure. Owing to the scarce brachiopod occurrences during this timespan, the occasional use of an open taxonomic nomenclature has been preferred in some taxa due to the limited available material and the inappropriate preservation, preventing the formal description of additional new taxa. This analysis also enables to elucidate the paleobiogeographical affinities of this new brachiopod fauna by analyzing the taxonomical similarity of the recorded assemblage with those from several well-documented basins from the NW-European (Euro-Boreal) and Mediterranean Tethyan bioprovinces (*sensu* Ager, 1967, 1971, 1973; Vörös 1977, 1984, 2005, 2016; Manceñido, 2002). It is worth noting that, in the Subbetic domain, the epigenetic dolomitization of most of the Hettangian–early Sinemurian carbonate successions virtually implies the absence of identifiable biostratigraphical markers. Therefore, the biostratigraphical correlations carried out in this work additionally enhances the knowledge on the chronostratigraphical range of Sinemurian brachiopods by providing new data on their very scarce occurrences in this interval, as also observed for the entire westernmost Tethys Ocean.

2. Geographical and geological setting

Brachiopods studied in the present work derive from the Venta Quesada section which outcrops in the south-eastern part of the Sierra Gorda mountain, around 550 m northwest of the road A-4153, and 11 km south-east of the Salar village, Granada Province, southern Spain (MGRS coordinates 30SVG079017, sheet 1025, Loja; Fig. 1). This area is geologically located in the central part of the Internal Subbetic (External Zones, Betic Cordillera; Fig.

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1(A)). The Lower Jurassic is represented by the Gavilán Fm. in this section, which consists of a thick carbonate succession that reaches over 300 m thickness in Sierra Gorda (García-Dueñas, 1969; Sandoval, 1983; García-Hernández et al., 1986).

According to Van Veen (1969), three members can be distinguished within the Gavilán Fm.: A basal one made up by dolostone sediments, a middle one constituted by ooidal to oncoidal limestone beds, and an upper member consisting of crinoidal limestone deposits. The dolomite member, with traces of algal laminations, is very homogeneous throughout the Subbetic and has been interpreted as being typical of tidal-flat environments (Olóriz et al., 2002), but it is not exposed in the Venta Quesada section.

In the middle member, sediments are characterized by a micritic peloidal mudstone to packstone microfacies, sometimes with oolitic/oncolitic grainstone to packstone beds and algal (dasycladacean, rhodophycean, and cyanophycean) wackestone layers (Fig. 2). In addition to algae, common fossils include larger foraminifera (mainly textulariids and lituolids), sponge spicules, bivalves (*Lithioperna* patches living half-buried in a vertical or oblique position to the surface, among other bivalves), gastropods, and echinoderms. Sedimentary structures such as bird-eyes and stylolites are also common. This benthic biota and sedimentary structures imply a shallow neritic marine depositional environment with occasional protected areas (Olóriz et al., 2002; Ruíz-Ortíz et al., 2004). The presence of oncolites and algae (photic zone), patches of *Lithioperna* in their living position and wackestone beds with larger benthic foraminifera involves low- or middle-energy environments in a rather protected platform (lagoon) or subtidal area. The oolites would indicate a depositional environment influenced by high energy hydrodynamics such as tidal-flat areas, whereas micrite content is typical of a platform environment and may come from the blue-green algae (cf. Olóriz et al., 2002; Ruíz-Ortíz et al., 2004).

The transition from the middle member to the upper crinoidal limestone is sudden. In the Venta Quesada section, crinoidal limestone deposits represent only two beds whose thickness varies laterally between 70 cm and 1 m. This crinoidal carbonate member bears the brachiopod assemblage studied herein (Figs. 2, 3). In the lower bed, brachiopods dominate over the crinoidal fragments, while in the upper bed the crinoids are dominant. Microfacies are represented by grainstone to packstone carbonates with dominant crinoids, brachiopods and bivalves (Fig. 3), sometimes with very scarce bryozoans and peloidal remains. In the Venta Quesada section, this crinoidal limestone member has not yielded any ammonites so far, but in some other Subbetic localities where crinoids are associated to more pelagic sediments they can locally occur (Rivas, 1979; Braga 1983), indicating the lower Pliensbachian (Rivas, 1979). Crinoidal limestone deposits are interpreted as high-energy deposits in external platforms, tidal to intertidal areas, that were accumulated during the diachronous progressive breaking-up suffered by the former pre-Pliensbachian carbonate platform (Olóriz et al., 2002).

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An unconformity surface with depositional hiatuses covering a large stratigraphic interval (at least Pliensbachian-upper Aalenian) marks the Lower-Middle Jurassic transition. Above this discontinuity, 30 cm of grey, partially nodular limestone beds provide uppermost Aalenian-lowermost Bajocian redeposited ammonites (*Graphoceras* sp., *Haplopleuroceras mundum*, and *Pseudaptetoceras klimakomphalum*). A new unconformity surface is found at the top of these sediments (Fig. 2), which is overlain by 4 m of grayish to yellowish compact to partially nodular limestone beds with scarce and unrepresentative ammonites (*Phylloceras* sp., *Holcophylloceras* sp.). This last stratigraphic interval shows wackstone microfacies with abundant thin-shelled bivalves assigned to the upper Bajocian-lowermost Bathonian interval in many other localities of the Subbetic swell habitats.

3. Material and methods

Amidst the profuse Jurassic outcrops widely known in the Betic Range, Sinemurian brachiopods are very scarce. To date, with the exception of fifteen specimens found by Pérez-López et al. (1993) in the lowermost Sinemurian, only the Sinemurian-Pliensbachian transition has yielded brachiopods in the eastern External Subbetic zone (Baeza-Carratalá and García Joral, 2012; Baeza-Carratalá, 2013). Consequently, the Venta Quesada section is so far the most prolific locality where Sinemurian brachiopods are recorded in the Internal Subbetic. In this outcrop, a total of 171 brachiopod specimens were collected. Supra-specific assignments follow the accepted determinations, published mainly in Kaesler and Selden (1997-2007). Recent supplementary data (Baeza-Carratalá, 2011, 2013) have been considered for the systematic assignement of some multicostate rhynchonellides into the genus *Alebusirhynchia*.

Whenever possible, the main biometric parameters (in mm) and indices were measured for the taxonomical analysis. The recrystallization of most of the material made the analysis of internal morphological characters practically unfeasible in all species. Only in some specimens of the genus *Alebusirhynchia* the internal features were poorly preserved. They were studied using the conventional method of taking acetate peels after making transverse serial sections (distance between serial sections: 0.1 mm). High resolution photomicrographs of acetate peels were taken using an optical microscope Nikon CFI60 E600POL. All specimens were coated with magnesium oxide prior to photographing.

All specimens figured and acetate peels are deposited in the collections of Earth and Environmental Sciences Department (University of Alicante, Spain). The ammonite zonal/subzonal standard scheme used follows Cariou and Hantzpergue (1997) and Aurell et al. (2002) for the Lower Jurassic of the Mediterranean Domain. Additional chronostratigraphical data, mainly from Sandoval (1983), were also used.

A taxonomical comparative analysis was performed after review of the dataset from several Mediterranean and NW-European basins. These brachiopod faunas were analyzed through

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cluster analysis with the UPGMA algorithm, using the Jaccard similarity coefficient from the PAST software package (Hammer et al., 2001) taking into account the presence *vs*. absence of the faunal elements from the Internal Subbetic Zone in several representative Mediterranean and Euro-Boreal basins.

4. Systematic paleontology

Phylum Brachiopoda Duméril, 1805

Subphylum Rhynchonelliformea Williams et al., 1996

Class Rhynchonellata Williams et al., 1996

Order Rhynchonellida Kuhn, 1949

Superfamily Rhynchonelloidea d'Orbigny, 1847

Family Rhynchonellidae d'Orbigny, 1847

Subfamily Piarorhynchiinae Shi et Grant, 1993

Genus *Cuneirhynchia* Buckman, 1918

Cuneirhynchia aff. *cartieri* (Oppel, 1861)

Fig. 4(1-4)

aff. 1861. *Rhynchonella cartieri* nov. sp. - Oppel, p. 545.

aff. 1889. *Rhynchonella cartieri* Oppel - Geyer, p. 63, pl. 7, figs. 13, 14; var. *rimata,* pl. 7, fig. 15.

aff. 1926. *Rhynchonella cartieri* Oppel - Peterhans, p. 363, pl. 2, figs. 1-4.

aff. 1943. *Rhynchonella cartieri* Oppel - Vigh, p. 45, pl. 2, figs. 25-27; pl. 3, figs. 1-5.

aff. 1992. *Cuneirhynchia*? *cartieri* (Oppel) - Dulai, p. 52, pl. 2, figs. 1, 2.

aff. 2003. *Cuneirhynchia cartieri* (Oppel) - Elmi et al., p. 701, pl. 4, figs. 10, 11.

aff. 2003. *Cuneirhynchia cartieri* (Oppel) - Vörös et al., p. 71, pl. 6, figs. 32-34.

aff. 2003. *Cuneirhynchia cartieri* (Oppel) - Dulai, p. 33, pl. 5, figs. 14-16; pl. 6; figs. 1-3.

aff. 2007. *Cuneirhynchia cartieri* (Oppel) - Vörös and Dulai, p. 54, pl. 1, fig. 20.

aff. 2007. *Cuneirhynchia cartieri* (Oppel) - Alméras et al., p. 73, pl. 4, figs. 7-8.

aff. 2008. *Cuneirhynchia cartieri* (Oppel) - Baeza-Carratalá, p. 81, pl. 1, figs. 3-5.

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aff. 2010. *Cuneirhynchia cartieri* (Oppel) - Mandl et al., p. 89, pl. 2, fig. 11.

Material: Ten specimens (SG1.CC1 to SG1.CC10) with varying state of preservation (Table 1).

Distribution: Hettangian–Sinemurian of the Transdanubian Ranges (Dulai, 1992, 2003; Vörös and Dulai, 2007); Sinemurian of the Northern Calcareous Alps (Vörös et al., 2003; Mandl et al., 2010); late Sinemurian (Raricostatum Zone)–early Pliensbachian (Aenigmaticum Zone) from Western Algeria (Elmi et al., 2003; Alméras et al., 2007); late Sinemurian–late? Pliensbachian from the easternmost External Subbetic zone (Baeza-Carratalá, 2008, 2013).

Description: Medium-sized equibiconvex to slightly dorsibiconvex shell with both valves rather flat and trigonal dorsal outline; length greater than width or nearly equidimensional, with the maximum width shifted towards the anterior margin. The beak is small, pointed and suberect, with a minute pedicle foramen. The beak ridges are well-developed, being sharper and longer on the ventral valve, limiting wide and smooth planareas. The lateral commissure is tilted toward the ventral valve, running close to the beak ridges of this valve or, at least, shifted with ventral orientation. The anterior one shows a rather wide and low fold giving a nearly rectimarginate aspect to the shell and showing wide deflections due to the strong ornamentation. Ribbing pattern consists of 7-9 robust ribs (exceptionally 11) running across the entire shell-length. Bifurcation is occasional and some thin growth lines are only perceptible in the planareas. The internal structure was not studied due to the recrystallization of the material.

Remarks: The specimens analyzed herein show criteria diagnostic of a *Cuneirhynchia* species (e.g., trigonal outline, lateral commissure closer to the ventral valve, wide planareas) but their ribbing pattern can be considered as "*forticostata*-type" (scarce, strong and broad ribs) which has not been reported in any previously described *Cuneirhynchia* species. Thus, this taxon could be regarded as a new species but, owing to the paucity of material and inappropriate individuals to analyze the internal structure, we cautiously favor an open nomenclature as *C.* aff. *cartieri*. Except for the ribbing pattern, *C. cartieri* (Oppel) shows closest affinities with the Subbetic specimens. The type-material, as it was defined by Oppel (1861), coincides with the individuals analyzed herein (fully ribbed shell, with narrow and thick dorsal and lateral outlines, respectively, and with beak ridges longer than *C. retusifrons*). Moreover, *C. cartieri* shows great variability in virtually all records integrated in the synonymy, mainly referred to the dorsal outline, convexity and thickness of the shell and the width of the dorsal median fold. This variability is recorded even within the same basin (Dulai, 1993, 2003; Alméras et al., 2007; Baeza-Carratalá, 2008). This intraspecific variability is explained in terms of different ecophenotypic factors, even in nearby platforms (Dulai, 1990, 1992, 2003). Thus, due to the apparently fast geographical evolution of this species, we cautiously do not split this stock from the well-known *C. cartieri*, awaiting further population data to be found in the future to improve the taxonomical accuracy.

On the other hand, the material recorded in the Venta Quesada section differs from several closer species assigned to Prionorhynchiinae, mainly by having trigonal and anteriorly

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truncated dorsal outline and the lateral commissure running closer to the ventral valve. In this sense, *Prionorhynchia gignouxi* shows nearly equibiconvex globose shells and wider planareas. These planareas are also wide and deeper in *P. gumbeli* which, in turn, shows a more densely-packed ribbing pattern as well as clearer and wider uniplication. *P. greppini* is easily identifiable due to its flatter lateral profile and the wide-expanded shells. The Subbetic material can be also separated from the representatives of the Triassic *Amoenirhynchia,* because this last genus does not develop coarse ribs on the entire shell.

Superfamily Rhynchotetradoidea Licharew, 1956

Family Prionorhynchiidae Manceñido et Owen, 2002

Genus *Prionorhynchia* Buckman, 1918

Prionorhynchia cf. *polyptycha* (Oppel, 1861)

Fig. 4(6)

cf. 1861. *Rhynchonella polyptycha* nov. sp. - Oppel, p. 544, pl. 12, fig. 4.

cf. 1889. *Rhynchonella polyptycha* Oppel - Geyer, p. 51, pl. 6, figs. 15-17.

non 1920. *Rhynchonella polyptycha* Oppel - Dareste de la Chavanne, p. 17, pl. 1, fig. 4.

cf. 1937. *Rhynchonella polyptycha* Oppel var. *multiplicata* - Ormós, p. 29, pl. 1, fig. 15.

? 1964. *Rhynchonella* cf. *polyptycha* Oppel - Sacchi-Vialli, p. 13, pl. 2, fig. 6.

cf. 1987. *Prionorhynchia polyptycha* (Oppel) - Alméras and Elmi, pl. 1, fig.13.

cf. 1992. *Prionorhynchia polyptycha* (Oppel) - Dulai, p. 48, pl. 1, fig. 5.

cf. 2003. *Prionorhynchia polyptycha* (Oppel) - Dulai, p. 14, pl. 5, figs. 1-3; cover, figs. 5-7.

cf. 2003. *Prionorhynchia polyptycha* (Oppel) - Vörös et al., p. 40, pl. 6, figs. 10-12.

cf. 2007. *Prionorhynchia polyptycha* (Oppel) - Vörös and Dulai., p. 54, pl. 1, fig. 8.

cf. 2008. *Prionorhynchia polyptycha* (Oppel) - Baeza-Carratalá, p. 134, pl. 2, fig. 4.

cf. 2009. *Prionorhynchia polyptycha* (Oppel) - Vörös, p. 65, pl. 8, fig. 3.

cf. 2010. *Prionorhynchia polyptycha* (Oppel) - Mandl et al., p. 89, pl. 1, fig. 12.

cf. 2011. *Prionorhynchia polyptycha* (Oppel) - Baeza-Carratalá et al., p. 146, fig. 4, 4.

Material: Only two disarticulated and very poorly preserved ventral valves (SG1.PP1 and SG1.PP2).

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Distribution: Early Sinemurian–early Pliensbachian from the Transdanubian Ranges (Vörös, 1993; Vörös and Dulai, 2007); Sinemurian from Northern Calcareous Alps (Vörös et al., 2003; Mandl et al., 2010); Pliensbachian from easternmost Subbetic area and the Internal Betic Zones (Emaciatum Chronozone, Elisa Subchronozone) (Baeza-Carratalá et al., 2011; Baeza-Carratalá, 2013).

Description: Small to medium-sized valves, subpentagonal in ventral outline; smooth and depressed planareas can be observed in lateral view, limited by a rather sharp ventral beak ridge. Despite of their poor state of preservation, the two ventral valves analyzed clearly evidence strong similarities with the species *P. polyptycha* (Oppel). Its ribbing pattern is also a distinctive attribute to assign these specimens to *P. polyptycha*. It consists of 16 dense ribs, commonly bifurcate on the flanks (Fig. 4(6)).

Remarks: The small to medium-sized shells recorded in Venta Quesada section are comparable to the mainly Sinemurian specimens recorded in the Transdanubian Ranges and the Northern Calcareous Alps (Dulai, 1992, 2003; Vörös et al., 2003; Vörös and Dulai, 2007). This stock probably finds their younger counterparts in the taxa attributed to *P. polyptycha* in the easternmost Subbetic area and in the Internal Betic Zone (Baeza-Carratalá 2008, 2013; Baeza Carratalá et al., 2011), although these occurrences are to some extent disconnected from the biostratigraphical range of the specimens analyzed herein. In this sense, the easternmost Subbetic and Internal Betic records are large-sized specimens related with the *P. quinqueplicata–P. serrata* group, mainly late Pliensbachian in age, reaching the Elisa Subchronozone of the Emaciatum Chronozone. The Algerian specimen attributed to *Rhynchonella polyptycha* (Dareste de la Chavanne, 1920) is not considered synonymous with the material studied herein, since this author illustrated a rather flat shell with strong and broad ribs.

Prionorhynchia polyptycha is similar to *P. greppini* but the former presents numerous closer ribs and seems to be more convex, whereas *P. gignouxi* differs in having narrower and more convex ovoid outline as well as a very different ribbing pattern. On the other hand, *P. serrata* is thicker and more convex, with stronger and broader ribs.

Superfamily Wellerelloidea Licharew, 1956

Family Wellerellidae Licharew, 1956

Subfamily Cirpinae Ager, 1965

Genus *Cirpa* De Gregorio, 1930

Cirpa subcostellata (Gemmellaro, 1882)

Fig. 4(5)

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1882. *Rhynchonella subcostellata* nov. sp. - Gemmellaro, p. 422, pl. 31, figs. 75-78.

? 1897. *Rhynchonella subcostellata* Gemmellaro - Böse, p. 193, pl. 14, fig. 9.

? 1912. *Rhynchonella subcostellata* Gemmellaro - Haas, p. 246, pl. 19, fig. 20.

2003. *Cirpa subcostellata* (Gemmellaro) - Dulai, p. 21, pl. 3, figs. 1-3.

2003. *Cirpa subcostellata* (Gemmellaro) - Elmi et al., p. 701, pl. 4, fig. 5.

2003. *Cirpa subcostellata* (Gemmellaro) - Vörös et al., p. 71, pl. 6, figs. 13-15.

2007. *Cirpa subcostellata* (Gemmellaro) - Vörös and Dulai, p. 54, pl. 1, fig. 12.

? 2007. *Cirpa subcostellata* (Gemmellaro) - Alméras et al., p. 45, pl. 2, figs. 8-10.

2008. *Cirpa*? aff. *subcostellata* (Gemmellaro) - Siblík and Lobitzer, p. 66, pl. 2, fig. 6.

2009. *Cirpa*? *subcostellata* (Gemmellaro) - Vörös, p. 76, pl. 8, fig. 9.

2010. *Cirpa*? *subcostellata* (Gemmellaro) - Mandl et al., p. 89, pl. 2, fig. 3.

Material: Four poorly preserved specimens (SG1.CS1 to SG1.CS4), three of them only showing partly incomplete double valves. A single specimen (SG1.CS1) can be measured, giving: L = 13.9 mm, W = 15.3 mm, T = 8.8 mm.

Distribution: Sinemurian–early Pliensbachian from Transdanubian Ranges (Vörös and Dulai, 2007); Sinemurian from Northern Calcareous Alps (Vörös et al., 2003; Mandl et al., 2010); late Sinemurian (Raricostatum Zone)–early Pliensbachian (Aenigmaticum Zone) from Western Algeria (Elmi et al., 2003; Alméras et al., 2007).

Description: Medium-sized dorsibiconvex shell, subpentagonal in dorsal outline. It is wider than long. Maximum width lies near the mid-length, giving a characteristic wide-expanded profile to the shell. Maximum thickness is located in the posterior third of the shell. The beak is erect and pointed with indiscernible pedicle foramen. The beak ridges are sharp but rather short, nearly imperceptible. The lateral commissure is arcuate near the beak, then running straight to the anterior margin. The anterior commissure is uniplicate with a narrow and trapezoidal dorsal median fold, slightly asymmetric in outline. Ribbing pattern consists of 14 sharp and densely-packed ribs, 4 of which are present on the median fold. Ribs are commonly bifurcated. Bifurcation is exposed from the posterior stages but also from the mid-length.

Remarks: The material herein analyzed suffered a slight diagenetic alteration, but several features such as the trapezoidal median fold, wide-expanded dorsal outline and the evidently bifurcated costation are diagnostic criteria to be attributed to the species *Cirpa subcostellata*. An exceptional description and discussion of the complete synonymy of *C. subcostellata* was comprehensively analyzed by Vörös (2009). We agree with the opinion of

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this author concerning the attributions made by Böse (1897) and Haas (1912), which should be questioned because of the presence of more convex valves. The Internal Subbetic specimens are in accordance with the material illustrated by Vörös et al. (2003) in the Northern Calcareous Alps, and Vörös and Dulai (2007) and Vörös (2009) in the Transdanubian Ranges, but the Subbetic specimens show lower and fairly wider folding pattern. Mandl et al. (2010) figured specimens with fewer bifurcated ribs than the material herein studied.

On the other hand, *C. subcostellata* shares several features with the earliest Jurassic stock of multicostate and bifurcate forms mainly represented by the genus *Jakubirhynchia* (Tomašových, 2006), but despite the fact that the internal structure of *C. subcostellata* remains unknown, this taxon has stronger and wider ribbing pattern than any species attributed to *Jakubirhynchia* so far (e.g., *J. latifrons, J. fascicostata, J. laevicosta*).

Genus *Salgirella* Moisseev, 1936

Salgirella albertii (Oppel, 1861)

Fig. 4(8-10)

1861. *Rhynchonella Albertii* nov. sp. - Oppel, p. 546, pl. 13, fig. 4.

1879. *Rhynchonella Albertii* Oppel - Uhlig, p. 32, pl. 4, fig. 1.

non 1879. *Rhynchonella Albertii* Oppel var. *Sospirolensis* - Uhlig, p. 32, pl. 4, fig. 2.

1889. *Rhynchonella Alberti* Oppel - Geyer, p. 43, pl. 5, figs. 14-17.

1889. *Rhynchonella Alberti* Oppel var. *lobata* - Geyer, p. 45, pl. 5, fig. 18.

non 1895. *Rhynchonella Alberti* Oppel - Fucini, p. 172, pl. 7, fig. 1.

non 1900. *Rhynchonella* aff. *Alberti* Oppel - Böse and Schlosser, p. 193, pl. 18, fig. 1.

?1910. *Rhynchonella Alberti* Oppel - Principi, p. 79, pl. 3, fig. 8.

non 1912. *Rhynchonella* nov. sp. ind. ex aff. *Alberti* Oppel - Haas, p. 241, pl. 19(1), fig. 16.

1920. *Rhynchonella Albertii* Oppel - Dareste de la Chavanne, p. 18, pl. 1, fig. 5.

1937. *Rhynchonella alberti var. lobata* Geyer - Ormós, p. 25, pl. 1, fig. 7.

non 1937. *Rhynchonella alberti* var. *minor* - Ormós, p. 25, pl. 1, figs. 8-9.

1993. *Salgirella* cf. *albertii* (Oppel) - Dulai, p. 30, pl. 1, fig. 2.

2002. *Salgirella alberti* (Oppel) - sensu Manceñido et al., p. 1266, fig. 862(1).

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2003. *Salgirella* cf. *albertii* (Oppel) - Dulai, p. 29, pl. 5, figs. 7-10.

2007. *Salgirella albertii* (Oppel) - Vörös and Dulai, p. 54, pl. 1, figs. 17, 18.

2008. *Salgirella albertii* (Oppel) - Baeza-Carratalá, p. 178, pl. 8, figs. 1-6.

2008. *Salgirella albertii* (Oppel) - Siblík and Lobitzer, p. 66, pl. 1, fig. 2.

2010. *Salgirella* cf. *albertii* (Oppel) - Mandl et al., p. 93, pl. 2, fig. 8; pl. 6, fig. 6.

2010. *Salgirella albertii* (Oppel) - Mandl et al., p. 91, pl. 7, fig. 6(9); pl. 9, fig. 5.

Material: Six articulated specimens (SG1.SA1 to SG1.SA6), including 3 juveniles.

Distribution: Hettangian–late Sinemurian from the Transdanubian Ranges (Dulai, 1993, 2003; Vörös and Dulai, 2007); Sinemurian from the Northern Calcareous Alps (Vörös et al., 2003; Siblík and Lobitzer, 2008; Mandl et al., 2010); Pliensbachian from the Eastern Subbetic (Baeza-Carratalá, 2008, 2013).

Description: Medium-sized dorsibiconvex shells (Table 1), triangular to pyriform in dorsal outline. W/L ratio is rather variable, but virtually all specimens show L>W. Thickness is about 3/5 of the length. Maximum width lies in the anterior third of the shell. Maximum thickness is observed near the mid-length or slightly shifted toward the posterior area. The beak is broad, strong, and erect to slightly incurved, with a minute pedicle foramen; the beak ridges are short and poorly-perceived, and do not develop planareas. The lateral commissure is straight and the anterior one is uniplicate, with a narrow and subtrapezoidal to arcuate dorsal median fold. Coarsely ribbed shell; ornamentation consists of 8-9 sharp ribs on each valve (except for the juvenile individuals), triangular in cross-section, without bifurcation, 3 of which being present on the median fold. There are smooth areas developed just adjacent to the median fold; in the Internal Subbetic material, these areas are less significant than in the type-material.

Remarks: *Salgirella albertii* shows great intraspecific variability in the literature referred in the synonymy list. This variability is also partially recorded in the Venta Quesada section. On the one hand, the specimens figured in Fig. 4(9-10) agree with the morphotype referred in the *Treatise* (Kaesler and Selden, 1997-2007) and several previous authors (Dareste de la Chavanne, 1920; Manceñido et al., 2002; partim Baeza-Carratalá, 2008), with larger and robust beak, lesser and stronger ribs, and narrower outline. On the other hand, the specimen herein figured in Fig. 4(8) fits better with the classical sense intended by Oppel, showing slightly wider outline, pointed beak and more patent smooth areas on the flanks of the dorsal median fold which is, in turn, more prominent. The outline of the dorsal median fold also varies with individuals from lower and subtrapezoidal to more arcuate and prominent. Ribbing pattern is rather consistent, with 8-9 ribs (5-6 in the juvenile specimens).

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Uhlig (1879) illustrated the variety *sospirolensis* which is not conspecific of *S. albertii* (Oppel), by having wide and deeper *Prionorhynchia*-type planareas. The same is applicable to the specimen figured by Principi (1910) which was tentatively allocated by Vörös (1994) to the genus *Homoeorhynchia.* Some previous authors figured specimens with a very flat dorsal valve (Fucini, 1895; Böse and Schlosser, 1900), some of them better matching with *Cirpa briseis*. Haas (1912) represented a specimen with a complex taxonomical combination: *Rhynchonella* nov. spec. ind. ex affin. *Alberti,* with a smooth posterior stage, updated as *Homoeorhynchia*? *lubrica* by Vörös (2009), whereas the morphotype *minor* (Ormós, 1937) shows flatter valves, densely-packed ribs, and wider uniplication.

The closer species is *Salgirella magnicostata* (Ormós, 1937), but the latter taxon is larger and with a strong ribbing pattern. On the other hand, the folding pattern of *Cirpa briseis* is comparable and usually difficult to distinguish from *S. albertii*, if we consider that they are usually recorded together in several Western Tethyan basins. In this sense, *S. albertii* develops wider smooth surfaces on both flanks of the dorsal median fold and shows more spaced ribs.

Genus *Calcirhynchia* Buckman, 1918

Calcirhynchia hungarica (Böckh, 1874)

Fig. 4(7)

1874. *Rhynchonella Hungarica* nov. sp. - Böckh, p. 139, pl. 4, figs. 5, 6.

2009. *Calcirhynchia*? *hungarica* (Böckh) - Vörös, p. 78, pl. 8, fig. 11 (*cum syn*.)

2010. *Calcirhynchia*? *hungarica* (Böckh) - Mandl et al., p. 91, pl. 2, figs. 4-6.

Material: Three specimens (SG1.CH1 to SG1.CH3); only two of them can be measured (Table 1).

Distribution: Hettangian–early Pliensbachian from the Transdanubian Ranges (Dulai, 1993; Vörös and Dulai, 2007; Vörös, 2009); Sinemurian from the Northern Calcareous Alps (Mandl et al., 2010); latest Sinemurian–earliest Pliensbachian of the External Betic Zone (Baeza-Carratalá and García Joral, 2012; Baeza-Carratalá, 2013; Baeza-Carratalá et al., 2014).

Description: The specimens recorded in the Venta Quesada section consist of small-sized equibiconvex shells, differing from the regular medium size that this species usually shows in other basins. They are subpentagonal with rounded margins in dorsal outline. Maximum width lies in the anterior margin. The beak is slightly curved and massive with imperceptible pedicle foramen. The beak ridges are not evidenced. The lateral flanks are flat and do not develop planareas. The lateral commissure is slightly arcuate near the beak, then running straight to the anterior margin. The anterior commissure is uniplicate (nearly rectimarginate)

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with a wide and very low dorsal median fold, trapezoidal to subrectangular in cross-section. There are 10-11 triangular ribs in each valve, densely-packed and without bifurcation, 4 of them occur on the median fold.

Remarks: The specimens recorded herein can be partly regarded as synonymous of those reported as *C. plicatissima* (Quenstedt) in the easternmost External Subbetic area (*partim* Baeza-Carratalá, 2008). Identical equivalence has been documented and updated in the Transdanubian Ranges and the Northern Calcareous Alps (Vörös, 2009; Mandl et al., 2010). The dorsal outline, the folding pattern and essentially the absence of planareas make the specimens found in the Venta Quesada section attributable to *C. hungarica* (Böckh) instead of *C. plicatissima* (see Tomašových, 2006, and Vörös 2009, for a wider discussion in this sense). Lacking a thorough revision of the profuse attributions to *C. plicatissima* in the Western Tethys as a whole, the synonymy list provided herein agrees with the detailed analysis carried out by Vörös (2009) on this species, and subsequent attributions to *C. hungarica*.

Calcirhynchia aff. *rectemarginata* (Vecchia, 1945)

Fig. 4(17-18)

aff. 1945. *Rhynchonella plicatissima rectemarginata* nov. sp. - Vecchia, p. 8, pl. 1, fig. 6.

aff. 1970. *Calcirhynchia rectemarginata* (Vecchia) - Gaetani, p. 375, pl. 29, figs. 1-8.

Material: Five specimens (SG1.CR1 to SG1.CR5); only two of them can be measured (Table 1).

Distribution: *C. rectemarginata* was recorded in the late Hettangian–early Sinemurian? from Lombardy (Gaetani, 1970).

Description: Medium-sized biconvex shells, rounded subtriangular to ovoidal in dorsal outline. Longer than width; maximum width is reached in the mid-length or slightly shift toward the anterior margin and the maximum convexity lies in the posterior third of the shell. The beak ranges from pointed and suberect (e.g., SG1.CR2 specimen) to stronger and incurved (SG1.CR1 specimen). Pedicle foramen is not visible. The beak ridges are short and poorly-developed. The lateral commissure is straight and there are not planareas on the lateral view. The anterior commissure is rectimarginate to vaguely uniplicate. In the uniplicate specimens, the dorsal median fold is very low and wide, almost occupying the entire anterior margin. The ribbing pattern consists of 12-14 coarse triangular ribs, densely-packed and without bifurcation. Spaced growth lines are occasionally noticed in two specimens.

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Remarks: The attribution to *C*. aff. *rectemarginata* is supported by the affinity of several external features such as the ribbing and folding patterns, the absence of planareas, and the presence of a clear rectimarginate anterior commissure. The intraspecific variability of the Internal Subbetic specimens is inherent to the grade of convexity of the valves. There are flatter and pointed-beak morphotypes comparable to those reported by Gaetani (1970). Conversely, some specimens evidence more globular shells with strong and more incurved beaks (Fig. 4(17)). The numerous specimens of this species from Lombardy (Gaetani, 1970) consistently shows sharper ribs than our morphotypes.

Similar multicostate rhynchonellide forms can be found in the Sinemurian *Rhynchonella canavarii* Fucini, 1893, but Alméras et al. (2007) illustrated this taxon with well-developed planareas and apparent anterior uniplication, suggesting their arrangement into the genus *Prionorhynchia*. Similarly, *C.* aff. *rectemarginata* can be clearly distinguished from *Prionorhynchia regia* (Rothpletz, 1886) recorded in the late Sinemurian–early Pliensbachian (Benhamou et al., 2000, Elmi et al., 2003; Alméras et al., 2007; Baeza-Carratalá, 2013), because the latter taxon has more ovoidal to pyriform profile and shallow but well-developed planareas. The similarity with congeneric forms was examined by Dulai (1993) who synonymyzed *C. rectemarginata* with *C. plicatissima,* then separated it from this group as *C. hungarica* (Vörös, 2009; Mandl et al., 2010).

Superfamily Hemithiridoidea Rzhonsnitskaia, 1956

Family Cyclothyrididae Makridin, 1955

Subfamily Cyclothyridinae Makridin, 1955

Genus *Alebusirhynchia* Baeza-Carratalá, 2011

Alebusirhynchia vorosi nov. sp.

Fig. 4(11-16)

Derivation of the name: Species dedicated to Attila Vörös, Hungarian geologist and well-known specialist of Mediterranean Jurassic brachiopods.

Types: specimen SG1.ANP1 (Fig. 4(11); Table 1) is designated as the holotype. One paratype (SG1.ANP7) has been sectioned (Fig. 5). Both the holotype and acetate peels are deposited at the Earth and Environmental Sciences Department collections (University of Alicante, Spain). Intraspecific variability is shown through the paratypes (Fig. 4(12-16)) and measured in Table 1 (SG1.ANP2 to SG1.ANP7).

Material: 56 specimens with diverse preservation states. All individuals show articulated but generally fragmented valves. Internal recrystallization is prevalent in all specimens.

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Type locality and horizon: In the Betic Range, this new species has been recorded in the crinoidal limestone member of the Gavilán Fm., which is attributed in the Venta Quesada section (Granada province) to the Turneri-Obtusum chronozones (without dismissing the earlier part of the Raricostatum Zone) of the Sinemurian.

Diagnosis: Small-sized, nearly equibiconvex multicostate rhynchonellide, ovoidal to subspherical in outline, with broad and strong beak and minute pedicle foramen. Lateral commissure ventrally inclined and the anterior one uniplicate, with a conspicuous trilobate profile. Strong, triangular, and widely-spaced ribbing pattern, without bifurcation. Dorsal median septum very short. Crural bases incipiently with dorsal orientation, developing raduliform crura afterwards, with inverted bracket-shaped crural endings, developed near the commissural plane.

Description:

External features (Fig. 4(11-16)). Small-sized equibiconvex shells (Table 1), longer than wide, showing (except for a few pyriform specimens) a subspherical to ovoidal dorsal outline. Thickness is about 3/4 of the length. Maximum thickness lies in the anterior third while maximum width lies near the mid-length of the shell. The beak is massive, strong, and slightly incurved, with a nearly imperceptible pedicle foramen; the beak ridges are noticed in the posterior third of the shell, developing smooth, wide, and shallow pseudoplanareas. The lateral commissure develops an incipient squama-glotta, running ventrally inclined afterwards. Anterior commissure is uniplicate, showing a rather narrow dorsal median fold, trapezoidal in cross-section. Two weakly-pronounced smooth areas are located on both flanks of the median fold, giving a slightly trilobate profile to the shell. Costation consists of 7 to 10 ribs on each valve, 2-3 (exceptionally 4) of which can be present on the median fold. Ribs are strong, widely-spaced and triangular in cross-section, without bifurcation. Spaced growth lines are only occasionally present and they are more conspicuous in the larger specimens.

Internal structure (Fig. 5). The intense recristallyzation of almost all material hinders accurate analysis of the internal architecture (Fig. 5(B)). Nevertheless, this species shows a subrectangular to ovoidal delthyrial cavity in cross-section, where neither pedicle collar nor deltidial plates are visible. Dental plates are short, arched and slightly divergent ventrally. Hinge teeth are massive with hardly discernible crenulations. They are inserted in broad sockets. The dorsal median septum is very short and nearly undetectable; traces of septalium unrevealed. Hinge plates are initially dorsally oriented and then subparallel, giving rise to crural bases early with dorsal orientation, developing raduliform crura afterwards, with inverted bracket-shaped crural endings developed near the commissural plane but, to some extent, shifted towards the ventral valve (Fig. 5).

Remarks: In addition to the main biometric ratios (Table 1), intraspecific variability mainly lies in the number of ribs present in each valve, and its location on the median fold. The development of the smooth area on both flanks of the median fold is also variable, thus

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varying the pronounced trilobate profile of the shell. The width of the median fold ranges from almost mid-width in some specimens up to wider and lower developments. On the other hand, maximum width can be slightly shifted toward the anterior third.

As can be deduced from the diagnostic criteria, this species matches with the generic diagnosis of the genus *Alebusirhynchia* (Baeza-Carratalá, 2011), specially attending to the beak features, the strong costation and the marked folding pattern, as well as the convexity of the valves. *Alebusirhynchia* was a monospecific genus hitherto, with *A. jorali* Baeza-Carratalá, 2011 as unique species recorded in the uppermost Sinemurian–lowermost Pliensbachian from the eastern Subbetic area. The closer affinity between both species is apparent, having in common several internal (e.g., short and arched dental plates, poorly-developed median septum, raduliform crura) and external (broad and strong beak, trilobate profile, ovoid outline, ribbing pattern) features. However, *A. jorali* shows labiate pedicle foramen and sharper ribs and the presence of denticula and well-developed crenulation of hinge teeth. Moreover, the population analyzed herein always consists of minute-sized individuals, showing specimens more pyriform in dorsal outline.

Among other Jurassic multicostate rhynchonellides, the closest affinities are found with *Gibbirhynchia*? *urkutica* (Böckh, 1874) which could even be contemporary with the Betic material, as it was recorded in the Sinemurian–early Pliensbachian from the Transdanubian basins (Dulai, 2003; Vörös and Dulai, 2007; Vörös, 2009). This species shares with the *Alebusirhynchia* stock an analogous ribbing pattern as well as their dorsal and lateral outlines, its dorsal fold being wider and lower and the internal structure remaining unknown. Finally, particular similarity is noticed with the folding and ribbing patterns observed in *Salgirella albertii* (Oppel, 1861), the latter species differing by having a flatter pedicle valve and more prominent ventral sulcus, whereas the *Alebusirhynchia* taxa are almost equibiconvex.

Order Terebratulida Waagen, 1883

Suborder Terebratulidina Waagen, 1883

Superfamily Loboidothyridoidea Makridin, 1964

Family Lobothyrididae Makridin, 1964

Subfamily Lobothyridinae Makridin, 1964

Genus *Lobothyris* Buckman, 1918

Lobothyris? *sospirolensis* (Uhlig, 1879) *sensu* Dulai (1993)

Fig. 6(1-2)

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1993. *Lobothyris*? *sospirolensis* (Uhlig) - Dulai, p. 39, pl. 2, fig. 2.

2003. *Lobothyris*? *sospirolensis* (Uhlig) - Dulai, p. 77, pl. 13, figs. 10-12.

Material: Nine mainly fragmented specimens (SG1.LS1 to SG1.LS9).

Distribution: Hettangian from the Transdanubian Ranges (Dulai, 1993, 2003; Vörös and Dulai, 2007).

Description: Small to medium-sized terebratulides, with equibiconvex, globose and much longer than wide shells (Table 1). They show an elliptical to subrectangular dorsal outline. The lateral margins are straight and subparallel and the anterior margin is straight. The thickness is commonly greater than the width. The beak is sharp and erect to slightly suberect. Pedicle foramen imperceptible. Beak ridges well-developed in the posterior third of the shell, also showing moderately depressed interareas. The lateral and anterior commissures are straight. Smooth shell except for some spaced growth lines.

Remarks: The species *Waldheimia sospirolensis* Uhlig, 1879 was tentatively attributed by Dulai (1993, 2003) and Vörös and Dulai (2007) to the genus *Lobothyris*, arguing that there are specimens with both dorsal median septum and without it in Uhlig's material. Unfortunately, the internal structure of the type-material remains unknown. Dulai (1993, 2003) recorded specimens externally homeomorphic with *W. sospirolensis*, and after performing serial sections, revealed a distinctive Loboidothyridoidea internal morphology, definitely analogous to that of the genus *Lobothyris,* and far from the zeilleriid-type structure.

Owing to this question, in this work, the taxonomical combination *Lobothyris*? *sospirolensis* (Uhlig, 1879) *sensu* Dulai (1993) is considered for the material collected from the Venta Quesada section, due to the external similarity shown with the material illustrated by Dulai (1993, 2003). Thus, in our specimens neither traces of a dorsal median septum nor dental plates are ascertainable as well. On the other hand, in the easternmost Subbetic area, Baeza-Carratalá (2008) recorded a few individuals assigned to *Zeilleria* sp. aff. *sospirolensis.* This material is clearly unrelated with the occurrences from the Venta Quesada section, since the external Subbetic individuals clearly show both dorsal median septum and dental plates and moreover a vague dorsal median sulcus is perceived giving to the shell a slightly bilobate aspect.

Lobothyris? *sospirolensis* is therefore herein regarded as a specific component of the "*Terebratula ovatissima*-type" group, which corresponds to elliptical to ovoidal *Lobothyris*, clearly longer than wide, with well-developed beak ridges and box-like profile. All records assigned to *Lobothyris ovatissima* (Quenstedt, *partim* 1856; *partim* 1871) are allocated to this stock, as well as *L. ovatissimaeformis* (Böckh, 1874; Gaetani, 1970; Siblík, 1993; Dulai, 1993, 2003; Vörös and Dulai, 2007) and related forms such as *Terebratula punctata* var. *ovatissima* Geyer, 1889.

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Lobothyris gr. *punctata* (Sowerby, 1813)

Fig. 6(3-5)

1813. *Terebratula punctata* nov. sp. - Sowerby, p. 46, pl. 15, fig. 4.

1966. *Lobothyris punctata* (Sowerby) - Siblík, p. 138, pl. 1, fig. 1.

1982. *Lobothyris punctata* (Sowerby) - Alméras and Moulan, p. 89, pl. 5, figs. 1-8.

1990. *Lobothyris punctata* (Sowerby) - Ager, p. 13, pl. 1, fig. 1.

1992. *Lobothyris punctata* (Sowerby) - Dulai, p. 65, pl. 4, fig. 2.

non 1999. *Lobothyris punctata* (Sowerby) - Iñesta, p. 26, pl. 7, fig. 5.

2003. *Lobothyris punctata* (Sowerby) - Vörös et al., p. 75, pl. 7, figs. 18-20.

2003. *Lobothyris punctata* (Sowerby) - Dulai, p. 74, pl. 13, figs. 7-9.

2007. *Lobothyris punctata punctata* (Sowerby) - Alméras et al., p. 88, pl. 6, figs. 5-11.

2008. *Lobothyris punctata* (Sowerby) - Baeza-Carratalá, p. 404, pl. 34, figs. 2, 3.

2009. *Lobothyris punctata* (Sowerby) - Vörös, p. 137, pl. 15, fig. 6 (*cum syn*.)

2010. *Lobothyris punctata* (Sowerby) - Mandl et al., p. 90, pl. 4, fig. 7.

Material: Six specimens with different state of preservation (SG1.LP1 to SG1.LP6).

Distribution: This taxon is recorded in the whole Western Tethys from the Sinemurian to the late Pliensbachian.

Description: This small to medium-sized stock of smooth terebratulides (Table 1) with a subcircular to pyriform dorsal outline suitably fits in the group of the species *Lobothyris punctata* due to the broad taxonomical concept that this taxon has acquired in the Western Tethys. In this sense, the Internal Subbetic individuals show a subcircular outline, maximum width in the mid-length and maximum thickness in the posterior third of the shell. The beak is erect to slightly curved, with a permesothyrid pedicle foramen. Beak ridges and interareas are not well-developed. Lateral and anterior commissures are straight. Weak growth lines are occasionally discernible.

Remarks: In the broad sense of this taxon, *Lobothyris punctata* is a pervasive species widely recorded in virtually all the Western Tethyan basins during the Early Jurassic. Ager (1990) carried out a comprehensive study on the British terebratulides, emphasizing the taxa included in the *Lobothyris punctata* group and its varieties. The synonymy list herein considered is far from being complete; we only have considered previous attributions in the

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Betic Range or nearby basins and those subsequently taken into account when performing the paleogeographical analysis. The specimens recorded in the Venta Quesada section show a subcircular outline in agreement with most of the Sinemurian records of this species (e.g., Dulai, 1992, 2003; Mandl et al., 2010). They are also similar to *Zeilleria alpina*, but external traces of dorsal median septum or dental plates are not perceived.

Suborder Terebratellidina Muir-Wood, 1955

Superfamily Zeillerioidea Allan, 1940

Family Zeilleriidae Schuchert, 1929 (in Schuchert and Le Ven)

Genus *Zeilleria* Bayle, 1878

Zeilleria venusta (Uhlig, 1879)

Fig. 6(6-8)

1879. *Waldheimia venusta* n. f. - Uhlig, p. 27, pl. 3, figs. 7, 8.

1889. *Waldheimia* cf. *venusta* Uhlig - Geyer, p. 24, pl. 3, figs. 14, 15.

1895. *Waldheimia venusta* Uhlig - Fucini, p. 149, pl. 7, figs. 22, 23.

1907. *Waldheimia venusta* Uhlig - Dal Piaz, p. 49, pl. 3, fig. 8.

1943. *Waldheimia venusta* Uhlig - Vigh, p. 29, pl. 1, figs. 5-7.

aff. 1992. *Zeilleria* aff. *venusta* (Uhlig) - Dulai, p. 74, pl. 5, fig. 4.

2003. *Zeilleria venusta* (Uhlig) - Dulai, p. 102, pl. 17, figs. 5-7; cover, 10-12.

aff. 2003. *Zeilleria* aff. *venusta* (Uhlig) - Dulai, p. 103, pl. 17, figs. 8-10.

2003. *Zeilleria venusta* (Uhlig) - Vörös et al., p. 76, pl. 7, figs. 35-37.

2007. *Zeilleria* aff. *venusta* (Uhlig) - Vörös and Dulai, p. 55, pl. 1, fig. 35.

2007. *Zeilleria venusta* (Uhlig) - Vörös and Dulai, p. 55, pl. 1, fig. 36.

aff. 2008. *Zeilleria* aff. *venusta* (Uhlig) - Baeza-Carratalá, p. 516, pl. 41, figs. 5-7.

2010. *Zeilleria venusta* (Uhlig) - Mandl et al., p. 90, pl. 6, fig. 2.

aff. 2014. *Zeilleria* aff. *venusta* (Uhlig) - Baeza-Carratalá and García Joral, p. 653, fig. 1, F1-F3.

Material: 46 articulated, mainly incomplete specimens (SG1.ZV1 to SG1.ZV46).

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Distribution: Sinemurian from Transdanubian Ranges (Vörös, 1993; Dulai, 2002, 2003; Vörös and Dulai, 2007), also attributing very close forms from this basin (*Zeilleria* aff. *venusta*) to the early Sinemurian (Dulai, 1992; Vörös and Dulai, 2007); Sinemurian from the Northern Calcareous Alps (Vörös et al., 2003; Mandl et al., 2010); Related forms are also recorded in the late Sinemurian–Pliensbachian from the easternmost Subbetic area (Baeza-Carratalá, 2008; Baeza-Carratalá and García Joral, 2014).

Description: Medium-sized (Table 1), nearly equibiconvex shells, subpentagonal elongated in dorsal outline and anterior margin truncated, giving a box-like appearance to the shell; longer than wide and considerably thick. The beak is suberect with a minute pedicle foramen. Maximum width and thickness are attained near the mid-length. The beak ridges are sharp and well-developed almost to the mid-length, developing clear shallow interareas. The lateral and anterior commissures are straight. Anterior outline typically rectangular with rounded edges. Smooth shell with dense growth-lines. The internal structure was not studied because of the poor preservation of the material, but traces of dorsal median septum and dental plates were ascertainable.

Remarks: *Zeilleria venusta* is one of the most abundant taxa in the Venta Quesada section. The individuals attributed to this species share most of the external features with the type-material (Uhlig, 1879) and those illustrated by Dulai (2003). A substantial difference with the type-material is the lesser developed beak ridges and the depth of planareas, which are shallower in most of the Internal Subbetic material. Their box-like profile and the sub-rectangular outline in anterior view make this species distinguishable from other zeilleriids with similar form. Baeza-Carratalá (2008) attributed to *Z.* aff. *venusta* specimens from the easternmost Subbetic area with the lateral commissure running close to the dorsal beak ridge. This feature is not noticed in the material analyzed herein. Concerning the shell profile, Dulai (1992, 2003) reported more rounded specimens in dorsal outline.

Among the closely related zeilleriid species, *Z. venusta* is rather similar to *Zeilleria stapia* and *Zeilleria batilla*, *Z. venusta* being more convex and thick, and *Z. batilla* having both valves flatter and more acute anterior margin. On the other hand, *Zeilleria mutabilis* presents a clear pentagonal and wider-expanded dorsal outline. In this sense, there is a minor stock in the Internal Subbetic material (e.g., SG1.ZV1; Fig. 6(6)) which does not exactly match the *Z. venusta* type. However, this stock has lesser subpentagonal outline than *Z. mutabilis*; additionally, they do not have subtriangular outline and the valves do not converge forming a sharper angle in the anterior margin as in the case of *Z. stapia*. Moreover, we cannot consider this stock as belonging to *Z. batilla* because the latter species has the maximum width noticeably shifted towards the anterior margin. Hence, we cautiously prefer considering this stock as belonging to the extreme range of variability of *Z. venusta*, these specimens being more widely expanded in the posterior half of the shell.

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5. Compositional analysis of the recorded assemblage

The Internal Subbetic assemblage partly agrees with the diversity pattern estimated by Sandy (1995) for the earliest Jurassic post-extinction fauna. Sandy (1995) recognized in this time interval assemblages dominated by generalist *Calcirhynchia, Zeilleria*, and *Lobothyris* species together with spiriferinids such as *Spiriferina walcotti*, representing a low-diversity fauna. In the Subbetic assemblage, spiriferinids are absent and rhynchonellides are the predominant group in species diversity, including seven species from six different genera (also showing diversification of the genus *Calcirhynchia*). Short-looped terebratulides are scarce and they are represented by two *Lobothyris* species, while long-looped zeilleriids are overrepresented in individuals (31.3%), all assigned to a single species. In this sense, the higher earliest Jurassic diversification is found in the Transdanubian Central Range where 5 rhynchonellide, 2 spiriferinide, and 7 terebratulide species are recorded from the Hettangian deposits, and 27 rhynchonellides, 16 spiriferinides, and 21 terebratulides from the early Sinemurian interval (Dulai, 2003).

6. Discussion

6.1. Paleobiogeographic affinities of the Betic Sinemurian brachiopod fauna

In the earliest Sinemurian times, the scant brachiopod occurrences previously reported in the shallow-water platform system established in the South-Iberian paleomargin (Pérez-López et al., 1993) reveals a clear affinity with those of the NW-European platforms. The former platform (which will give rise to the Internal Subbetic swell afterwards) was placed in the more offshore areas of the Betic Domain and, as a result, representative faunal elements from the NW-European basins widely spread throughout the continuous and homogeneous shallow-water platform habitats. Thus, *Calcirhynchia calcaria* and *C. calcicosta*, profusely recorded in the British and French basins (e.g., Ager, 1958, 1962; Alméras and Hanzo, 1991), were also recorded in the pre-Pliensbachian Betic platform system (Pérez-López et al., 1993).

A paleobiogeographical analysis has been carried out, comparing brachiopod faunas from several Mediterranean and NW-European basins through a cluster analysis computed using the Jaccard similarity coefficient (Figs. 7, 8(A)). It must be taken into account that the most prolific occurrences in the considered basins correspond to the early Sinemurian interval, the easternmost Subbetic assemblages being a bit younger (late Sinemurian–earliest Pliensbachian). The analysis reveals that the effective disruption of the NW-European influences in the South-Iberian paleomargin is detected in the Sinemurian, earlier than expected by previous authors such as Baeza-Carratalá (2013), leading to recognize the well-established Mediterranean/Euro-Boreal duality in brachiopods provinciality (Vörös, 2016). Hence, the Venta Quesada assemblage, notwithstanding its paleogeographical situation nearby to the proto-Atlantic Ocean (Fig. 8(A)), shows greater affinity with the most intra-Tethyan basins with Mediterranean character such as the Transdanubian Ranges (Dulai,

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1992, 1993, 2003; Vörös and Dulai, 2007) where 80% of the taxa or very close species are present, and with the Northern Calcareous Alps (e.g., Geyer, 1889; Vörös et al., 2003; Mandl et al., 2010) sharing 70% of the taxa (Table 2, Fig. 7). This Mediterranean cluster also comprises the eastern External Subbetic fauna (Baeza-Carratalá, 2013), regarded as a peri-Mediterranean type basin by Vörös (2016), having in common 6/10 taxa with the Internal Subbetic assemblage (Table 2).

The affinity with the North-African basins is detected through the species *Cirpa subcostellata* and maybe *Cuneirhynchia* aff. *cartieri* (Elmi et al., 2003; Alméras et al., 2007) from Western Algeria. Also noteworthy is the minimal affinity with the rest of the peri-Iberian platform such as the Asturian (Comas-Rengifo and Goy, 2010) and the Pyrenean basins (Alméras and Fauré, 2000), only detected by means of the pervasive *Lobothyris punctata*, a cosmopolitan and catchall species widely recorded in the entire Western Tethys Ocean (Table 2, Fig. 7). Thus, considering this taxon, the same affinity is accomplished with other NW-European areas such as the South-Armorican Massif (Alméras et al., 2010). On the other hand, the Portuguese Sinemurian assemblages (Paredes et al*.,* 2013) recorded in the Oxynotum–Raricostatum chronozones of the Lusitanian Basin, do not include any faunal element in common with the Internal Subbetic assemblage (Table 2). This fact evidences that, at this time, the free interconnection between the South-Iberian paleomargin and the NW-European platforms was not effective, emphasizing therefore the Mediterranean affinity of the Subbetic area.

Consequently, a clear Mediterranean/Euro-Boreal dichotomy is revealed in the cluster analysis, splitting the faunas with a clear Mediterranean biogeographical affinity (i.e., Transdanubian Ranges, Northern Calcareous Alps, and the Subbetic Domain – Internal and External Zones) from the other cluster representing the Euro-Boreal realm (Portuguese and North-Iberian Paleomargin faunas together with that of the South Armorican Massif; Fig. 7). The Western Algeria brachiopod fauna might evidence an intermediate affinity, subsequently revealed afterwards in the Pliensbachian as a marginal Euro-Boreal Basin *sensu* Vörös (2016). Finally, it is worth noting the similarity detected between the Hettangian assemblage reported from Lombardy (Gaetani, 1970) and the Internal Subbetic one. The assemblage from Bergamo has been excluded from the paleogeographical analysis because it was recorded from the upper Hettangian and the taxonomical composition is rather different at the specific level. However, the Lombardian assemblage is made of *Cuneirhynchia latesinuata, Calcirhynchia rectemarginata, Lobothyris ovatissimaeformis*, and *Zeilleria perforata,* revealing unequivocal signs of similitude at the morphotype level with Mediterranean assemblages.

6.2. Significance of the Internal Subbetic assemblage with respect to the first Jurassic brachiopod diversification in the Betic Ranges

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Prior to the end-Triassic extinction event, the brachiopod record in the Betic Ranges is very limited due to several, mainly lithostratigraphical factors. On one hand, in the mainly metamorphic Internal Zones, the only brachiopod evidence in this area is restricted to the indefinite exceptional remains of a few cross-sections in the Early Devonian of the Nevado-Filábride complex (Laborda-López et al., 2015). On the other hand, the siliciclastic and evaporitic units of Buntsandstein and Keuper facies are not suitable to the brachiopod record and only in the epicontinental carbonates of Muschelkalk facies, evident occurrences of the endemic genus *Misunithyris* are reported in the lower Ladinian (Baeza-Carratalá et al., 2018).

A relatively comparable situation occurred after the end-Triassic mass extinction event in the External Betic Zones. The epigenetic dolomitization in most of the Hettangian–early Sinemurian carbonate successions represented by the lower member of the Gavilán Fm. (Van Veen, 1969) virtually implies the absence of any identifiable brachiopods. Even so, Pérez-López et al. (1993) recorded in these dolomitic facies the remarkable occurrence of a monotypic assemblage of the genus *Calcirhynchia* (only 15 specimens attributed to *C. calcaria* and *C. calcicosta*). These brachiopod-bearing sediments were dated by Pérez-López et al. (1993) to the lowermost Sinemurian Bucklandi–Semicostatum chronozones (Fig. 8(B)). Both *Calcirhynchia* species are widely recorded in the Hettangian–early Sinemurian of the British and French basins (e.g., Ager, 1958, 1962; Alméras and Hanzo, 1991). This record is in accordance with the paleogeographical situation of the pre-Pliensbachian platform (which developed the Internal Subbetic swell afterwards) in the most offshore Betic domain, thus facilitating a free connection with the NW-European platforms.

As it is well known, this homogeneous platform system established in the Western Tethys subsequently drowned (e.g., Bernoulli and Jenkyns, 1974; Winterer and Bosselini, 1981). Prior to the well-known horst/graben demarcation in the Subbetic Domain (Internal, Median and External Subbetic), an initial pre-rifting stage of the westernmost Tethyan platforms occurred (Vera, 1988, 1998; Molina et al., 1999), which has been interpreted as the first tectonic pulses into the Sinemurian (Nieto, 1997; cf. Ruiz-Ortiz et al., 2004; Tent-Manclús, 2006), with incipient irregular topographic bottoms, thus diversifying the ecological niches and facilitating the establishment of stable brachiopod communities (Baeza-Carratalá, 2013). So far, in the Betic Range, the first brachiopod diversity peak with a remarkable speciation and radiation episode was recorded in the Raricostatum–Aenigmaticum chronozones (Fig. 8(B)), corresponding to the latest Sinemurian–earliest Pliensbachian (Baeza-Carratalá and García Joral, 2012; Baeza-Carratalá, 2013) and typified by endemic species such as *Lycnothyris lancisi, Cincta peiroi, Alebusirhynchia jorali*, and *Praespheroidothyris cisnerosi*, the representative stock of the multicostate zeilleriids, and a number of taxa of mainly Mediterranean affinity (mostly evident through several species of *Securina, Prionorhynchia, Cuneirhynchia*, and ribbed spiriferinids [= Assemblage 1] in Baeza-Carratalá, 2013). This assemblage pointed to the initial disconnection of the Mediterranean and Euro-Boreal brachiopod paleobioprovinces in the Betic Domain.

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With the new data analyzed herein, it can be ascertained that the aforementioned initial diversification and the onset of the Mediterranean affinity in the brachiopod assemblages from the Subbetic area took place earlier than the Raricostatum–Aenigmaticum biochronozones. As can be deduced from the biostratigraphical distributions of the identified taxa, the assemblage recorded in the Venta Quesada section can be considered as Sinemurian in age and is highly diversified, since the 171 specimens collected have been arranged into 10 species belonging to six different superfamilies (four rhynchonellides, one terebratulides and one zeilleriids). Thus, this assemblage can be regarded as representative of the early diversification of the brachiopod fauna in the Betic Range as a whole, since it is the oldest Sinemurian assemblage recorded with several genera occurring together.

It is widely recognized in the entire Betic Ranges that the levels from which this assemblage derives are stratigraphically overlying the lower dolomitic member of the Gavilán Fm., where the *Calcirhynchia* occurrences were dated in the Bucklandi–Semicostatum chronozones. Owing to the Sinemurian–Pliensbachian transition (Raricostatum–Aenigmaticum chronozones) can be calibrated with the aforementioned Assemblage 1 of brachiopods (Baeza-Carratalá and García Joral, 2012; Baeza-Carratalá, 2013), which is absent in the Internal Subbetic, it is very likely that the assemblage from the Venta Quesada section (Fig. 8(B)) typifies the Turneri–Obtusum chronozones interval (without dismissing the earlier part of the Raricostatum zone). This interval concurs with the early and progressive diversification noticed in several Tethyan and NW-European basins from the Hettangian–early Sinemurian times onwards (Rossi-Ronchetti and Brena, 1953; Gaetani, 1970; Alméras and Hanzo, 1991; Dulai, 1993, 2001, 2003; Siblík, 1999; Böhm et al., 1999; Tomašových, 2006), coinciding, as mentioned above, with the development of incipient modification of the sea-bottom, thus diversifying the eco-spaces and enabling the diversification of brachiopod communities.

This biostratigraphical approach also allows refining the dating of earliest Jurassic sediments in the Sierra Gorda region. Previous authors (Sandoval, 1983; Linares and Sandoval, 1993) provided the earliest accurate chrono-records in the hardground surface overlying the Early Jurassic deposits, dating from the late Aalenian, and then in the Bajocian–early Bathonian interval (Fig. 3). The carbonate platform succession underlying this unconformity was roughly attributed to the "middle Liassic" (Sandoval, 1983; Linares and Sandoval, 1993) or, at most, to the pre-Domerian interval. Thus, the stratigraphical hiatus spanning the earliest and Middle Jurassic deposits was not accurately calibrated. The brachiopod assemblage analyzed herein enables us to refine this depositional hiatus (Fig. 3). The biochronostratigraphical gap actually spans from the Turneri-Obtusum (lowermost Raricostatum?) chronozones (inferred from the brachiopod assemblage analyzed herein) to the Aalenian-earliest Bajocian deduced from the ammonite occurrences (*Graphocreas* sp., *Haplopleuroceras mundum*, and *Pseudaptetoceras klimakomphalum*).

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7. CONCLUSIONS

The newly discovered Sinemurian brachiopod assemblage from the Internal Subbetic Zone (Granada province, Betic Range, Spain) yielded 10 different taxa (7 rhynchonellides and 3 terebratulides) reported for the first time in this area. Taxonomical analysis allows for the formal establishment of a new rhynchonellide species, *Alebusirhynchia vorosi* nov. sp., detailing its external and internal structures. The paucity of material and the inappropriate preservation prevent the formal description of other new taxa such as *Cuneirhynchia* aff. *cartieri* and *Calcirhynchia* aff. *rectemarginata,* cautiously adopting an open taxonomic nomenclature.

This assemblage represents the first step in the evolutionary diversification of Mediterranean Lower Jurassic brachiopods in the Betic Ranges and the recovery of the background conditions for the establishment of diversified brachiopod communities after the end-Triassic mass extinction event in the External Betic Zones. It is the oldest assemblage recorded in the Sinemurian with several genera occurring together, after the Euro-Boreal monogeneric assemblage reported by previous authors in the earliest Sinemurian.

The Mediterranean affinity of this assemblage, recorded in the more offshore areas of the Betic Domain, reveals that the onset of the Mediterranean/Euro-Boreal bioprovinciality and the initial brachiopod diversification in the pre-Pliensbachian Internal Subbetic platform took place earlier than expected, in the Turneri–Obtusum (and lowermost Raricostatum?) chronozones, coeval with the early and progressive diversification noticed in several intra-Tethyan basins such as the Northern Calcareous Alps and the Transdanubian Ranges from the Hettangian–early Sinemurian times onwards. Consequently, a remarkable speciation and radiation episode is documented as precursor of the peak of brachiopod diversity reported in the latest Sinemurian–earliest Pliensbachian in the Subbetic domain as a whole, coinciding with one of the pre-rifting platform pulses, thus diversifying the eco-spaces and enabling the diversification of brachiopod communities.

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Table and Figure captions

Table 1. Biometric parameters of measurable specimens for the studied taxa from the Internal Subbetic Zone. L: length; W: width; T: thickness; R: number of ribs. (1) Holotype; (2) Specimen sectioned in this work.

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Taxon	Specimen	L	W	T	W/L	T/L	T/W	R
Cuneirhynchia aff. *Cartieri* (Oppel, 1861)	SG1.CC1	12.2	11.9	8.2	0.97	0.68	0.69	8
	SG1.CC2	14.4	12.4	9.1	0.86	0.63	0.73	8
	SG1.CC3	11.5	10.1	9.2	0.88	0.80	0.91	7
	SG1.CC4	11.2	11.1	9.5	0.99	0.85	0.85	9
	SG1.CC5	-	13.2	9.0	-	-	0.68	11
	SG1.CC6	10.5	8.7	6.9	0.82	0.66	0.80	8
	SG1.CC7	11.1	10.7	8.1	0.97	0.73	0.75	8
Salgirella albertii (Oppel, 1861)	SG1.SA1	14.8	13.0	8.9	0.88	0.60	0.68	8
	SG1.SA2	13.9	11.9	8.2	0.86	0.58	0.68	8
	SG1.SA3	15.2	12.0	-	0.79	-	-	9
	SG1.SA4	7.1	6.6	4.5	0.92	0.63	0.68	5
	SG1.SA5	7.6	7.6	4.8	1.01	0.63	0.63	6
Calcirhynchia hungarica (Böckh, 1874)	SG1.CH1	7.2	7.3	4.6	1.01	0.64	0.63	10
	SG1.CH2	10	8.9	7.8	0.89	0.78	0.88	11
Calcirhynchia aff. *Rectemarginata* (Vecchia, 1945)	SG1.CR1	13.6	11.9	9.1	0.87	0.67	0.76	12
	SG1.CR2	11.0	9.1	5.8	0.83	0.53	0.64	12
Alebusirhynchia vorosi nov. sp.	SG1.ANP1[(1)]	8.9	7.3	6.1	0.82	0.69	0.84	7
	SG1.ANP2	8.9	6.9	6.4	0.77	0.71	0.92	7
	SG1.ANP3	8.0	7.6	6.3	0.95	0.79	0.83	7
	SG1.ANP4	8.9	7.7	6.1	0.86	0.68	0.80	8
	SG1.ANP5	9.7	8.6	7.0	0.89	0.72	0.79	9
	SG1.ANP6	12.7	11.1	9.5	0.87	0.75	0.86	9
	SG1.ANP7[(2)]	8.5	7.3	5.7	0.86	0.67	0.78	7
	SG1.ANP8	8.5	7.9	7.3	0.93	0.85	0.92	10
	SG1.ANP9	9.7	8.4	7.0	0.87	0.73	0.83	9
	SG1.ANP10	9.1	8.1	5.9	0.91	0.65	0.72	9
	SG1.ANP11	10.1	9.2	7.1	0.91	0.71	0.77	8
	SG1.ANP12	8.8	9.1	7.3	1.03	0.83	0.80	7
	SG1.ANP13	9.0	8.0	6.3	0.89	0.69	0.78	7
	SG1.ANP14	8.6	8.1	7.4	0.94	0.87	0.92	9
	SG1.ANP15	8.2	7.6	6.4	0.93	0.78	0.83	7
	SG1.ANP16	9.2	8.7	6.5	0.94	0.71	0.75	7
	SG1.ANP17	8.2	7.7	6.7	0.94	0.82	0.87	7
	SG1.ANP18	8.7	7.8	5.8	0.89	0.67	0.75	7

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Table 2. List of Sinemurian brachiopod taxa found in the Internal Subbetic Zone and their occurrence (x) in several representative Mediterranean and Euro-Boreal basins. Data from: External Subbetic: Baeza-Carratalá (2008, 2013); Transdanubian Ranges: Dulai (2003), Vörös and Dulai (2007); Western Algeria: Elmi et al. (2003), Alméras et al. (2007); Lusitanian Basin: Paredes et al. (2013); Northern Calcareous Alps: Geyer (1889), Vörös et al. (2003), Mandl et al. (2010); South-Armorican Massif: Alméras et al. (2010); Asturian Basin: Comas Rengifo and Goy (2010); Pyrenees: Alméras and Fauré (2000) (additional data sources in the text). Species shared with the Internal Subbetic assemblage are given in total number of taxa and as percentages of the number of Internal Subbetic taxa (within parentheses).

Internal Subbetic (herein)	External Subbetic	Trans-danubian Ranges	Western Algeria	Lusitanian Basin	Northern Calcareous Alps	South-Armorican Massif	Asturian Basin
Cuneirhynchia aff. *cartieri*	x	x	x		x		
Prionorhynchia cf. *polyptycha*	x	x			x		
Calcirhynchia hungarica	x	x			x		
Calcirhynchia aff. *rectemarginata*							
Cirpa subcostellata		x	x		x		
Salgirella albertii	x	x			x		
Alebusirhychia vorosi nov. sp.							
Lobothyris gr. *punctata*	x	x	x		x	x	x
Lobothyris? *sospirolensis*		x					
Zeilleria venusta	x	x			x		
ss 10	6 (60%)	8 (80%)	3 (30%)	0 (0%)	7 (70%)	1 (10%)	1 (10%)

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Fig. 1. A. Geological sketch map showing the studied area within the context of the Betic Cordillera (modified after Vera et al., 2004). B. Map showing the location of Venta Quesada section (1) among the Jurassic outcrops in the vicinity of Granada (Southern Spain).

Fig. 2. Lower–Middle Jurassic lithostratigraphical section showing the ammonites and brachiopod occurrences in the Venta Quesada locality.

Fig. 3. Levels with brachiopods in the Venta Quesada Section. A. Hand-sample detail of the crinoidal grainstone deposits containing abundant rhynchonellide species. B. Photomicrograph of the crinoidal carbonate member of the Gavilán Fm., showing microfacies represented by grainstone to packstone carbonates with dominant crinoidal fragments, and brachiopod and bivalve remains. Scale bars: 2 cm (A), 1 mm (B).

Fig. 4. Representative rhynchonellide species of the Internal Subbetic Sinemurian assemblage. 1–4. *Cuneirhynchia* aff. *cartieri*. 1: specimen SG1.CC1; 2: specimen SG1.CC2; 3: specimen SG1.CC3; 4: specimen SG1.CC4. 5. *Cirpa subcostellata* (Gemmellaro), specimen SG1.CS1. 6. *Prionorhynchia* cf. *polyptycha* (Oppel), specimen SG1.PP1. 7. *Calcirhynchia hungarica* (Böckh), specimen SG1.CH1. 8–10. *Salgirella albertii* (Oppel). 8: specimen SG1.SA1; 9: specimen SG1.SA2; 10: specimen SG1.SA3. 11–16. *Alebusirhynchia vorosi* nov. sp. 11: specimen SG1.ANP1, holotype; 12: specimen SG1.ANP2, paratype; 13: specimen SG1.ANP3, paratype; 14: specimen SG1.ANP4, paratype; 15: specimen SG1.ANP5, paratype; 16: specimen SG1.ANP6, paratype. 17, 18. *Calcirhynchia* aff. *rectemarginata* (Vecchia). 17: specimen SG1.CR1; 18: specimen SG1.CR2. All specimens were coated with magnesium oxide. Views of each specimen are ordered consecutively in dorsal (a), lateral (b), anterior (c), and ventral (d) views. Scale bar: 1 cm.

Fig. 5. Internal structure of *Alebusirhynchia vorosi* nov. sp. A. Transverse serial sections through the SG1.ANP7 specimen from the Venta Quesada section (distance from the beak in mm). B. Photomicrographs of acetate peels obtained from the same specimen. B_1: Section at 0.6 mm from the apex, showing arched and slightly ventrally divergent dental plates; B_2: Section at 1.3 mm from the apex, showing the early stage of cardinalia with incipient hinge plates; B_3, B_4: Sections at 1.5 and 1.6 mm from the apex, respectively, showing hinge teeth, sockets, and crural bases development. cb: crural bases; dp: dental plates; hp: hinge plates; ht: hinge teeth; s: socket. Scale bars: 3 cm (A), 500 µm (B_1–B_4).

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Fig. 6. Representative terebratulide species of the Internal Subbetic Sinemurian assemblage. 1, 2. *Lobothyris*? *sospirolensis* (Uhlig) *sensu* Dulai. 1: specimen SG1.LS1; 2: specimen SG1.LS2; 3–5. *Lobothyris* gr. *punctata* (Sowerby). 3: specimen SG1.LP1; 4: specimen SG1.LP3; 5: specimen SG1.LP2. 6–8. *Zeilleria venusta* (Uhlig). 6: specimen SG1.ZV1; 7: specimen SG1.ZV2; 8: specimen SG1.ZV3. All specimens were coated with magnesium oxide. Views of each specimen are ordered consecutively in dorsal (a), lateral (b), and anterior (c) views. Scale bar: 1 cm.

Fig. 7. Faunal similarity cluster analysis performed on the Sinemurian brachiopod assemblages (sources in the text) using the Jaccard similarity index, taking into account the occurrences of brachiopod species from the Internal Subbetic Zone in several representative Mediterranean and Euro-Boreal basins. This multivariate approach is interpreted in terms of paleobiogeographical affinity. The star marks the assemblage described herein.

Fig. 8. Palaeogeographical and chronostratigraphical context of the studied outcrops. A. Location of the different brachiopod faunas compared and referred to in this study, plotted on an Early Jurassic palaeomap, slightly modified after Bassoullet et al. (1993). B. Sketch showing the Sinemurian biochronozones commonly used for the Betic Range, and their equivalent in the Western Tethys Domain as a whole, showing the occurrence of brachiopod assemblages in the Betic Ranges (1: Pérez Lopez et al., 1993; 2: this study; 3: Baeza-Carratalá, 2013).

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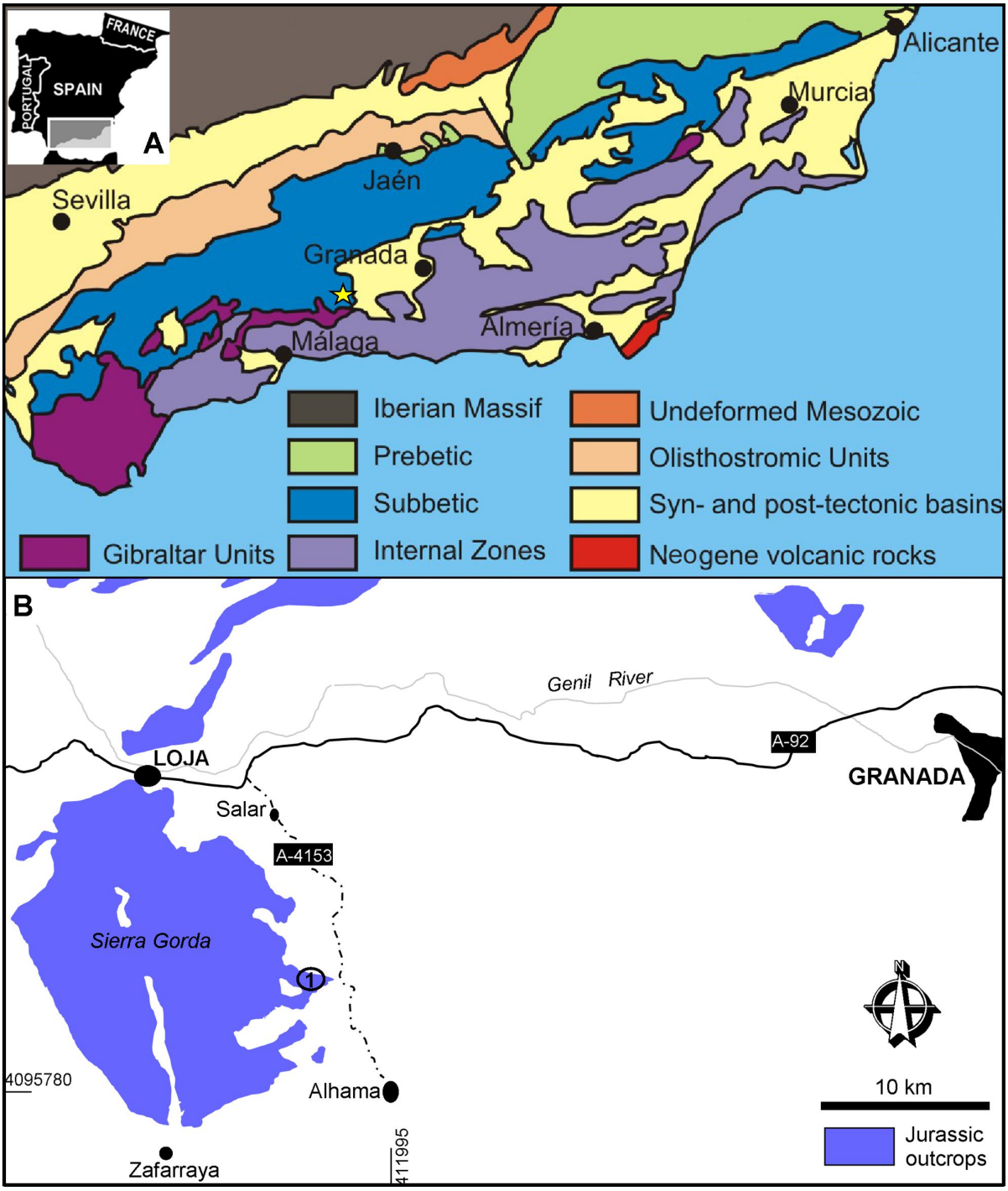

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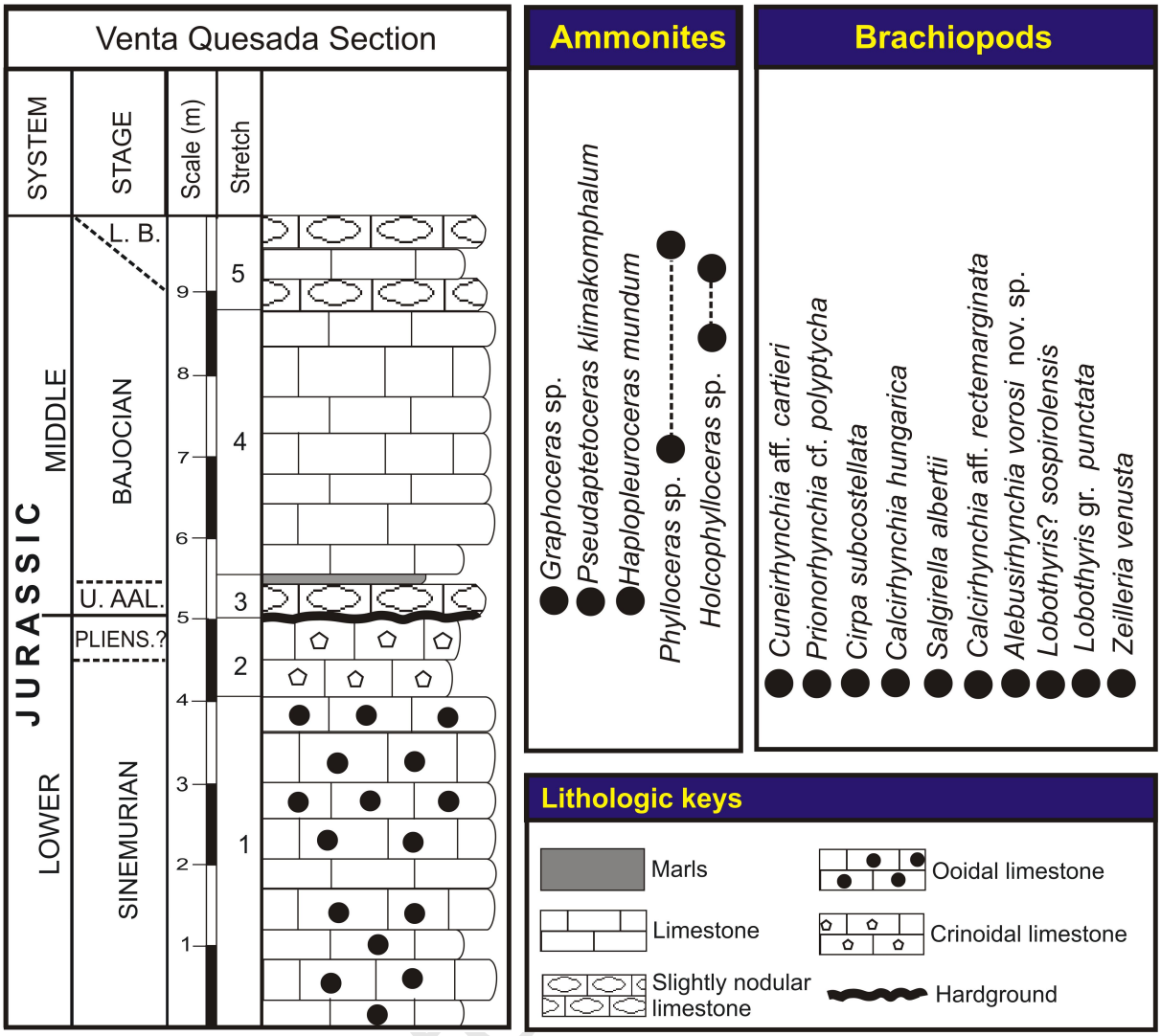

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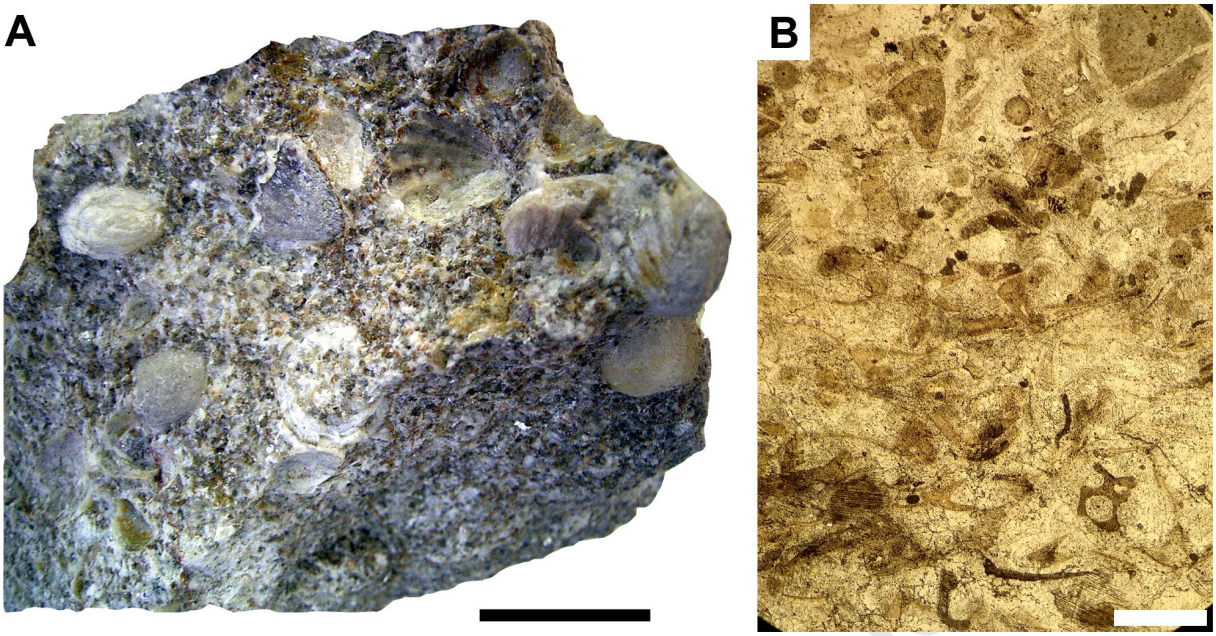

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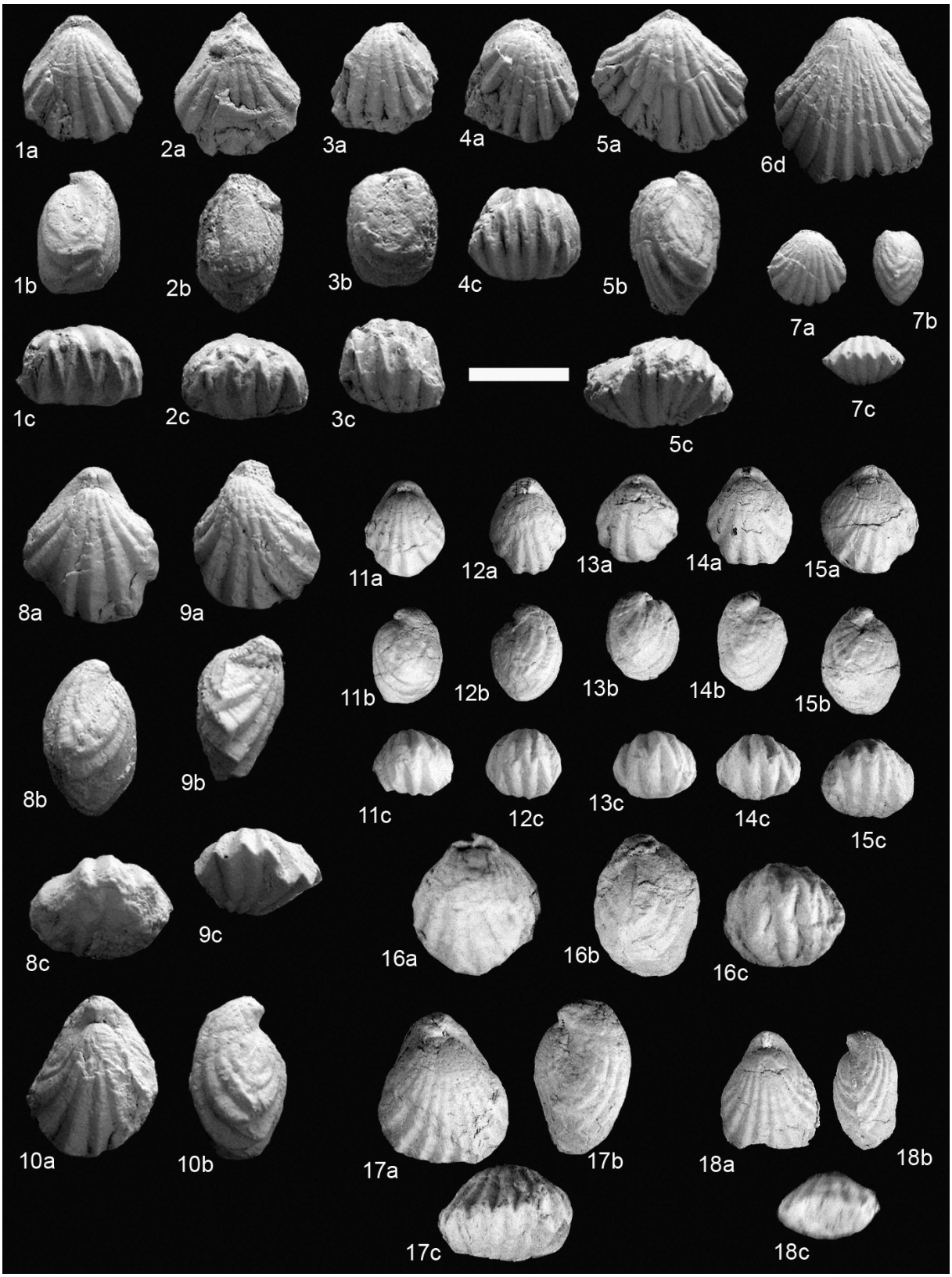

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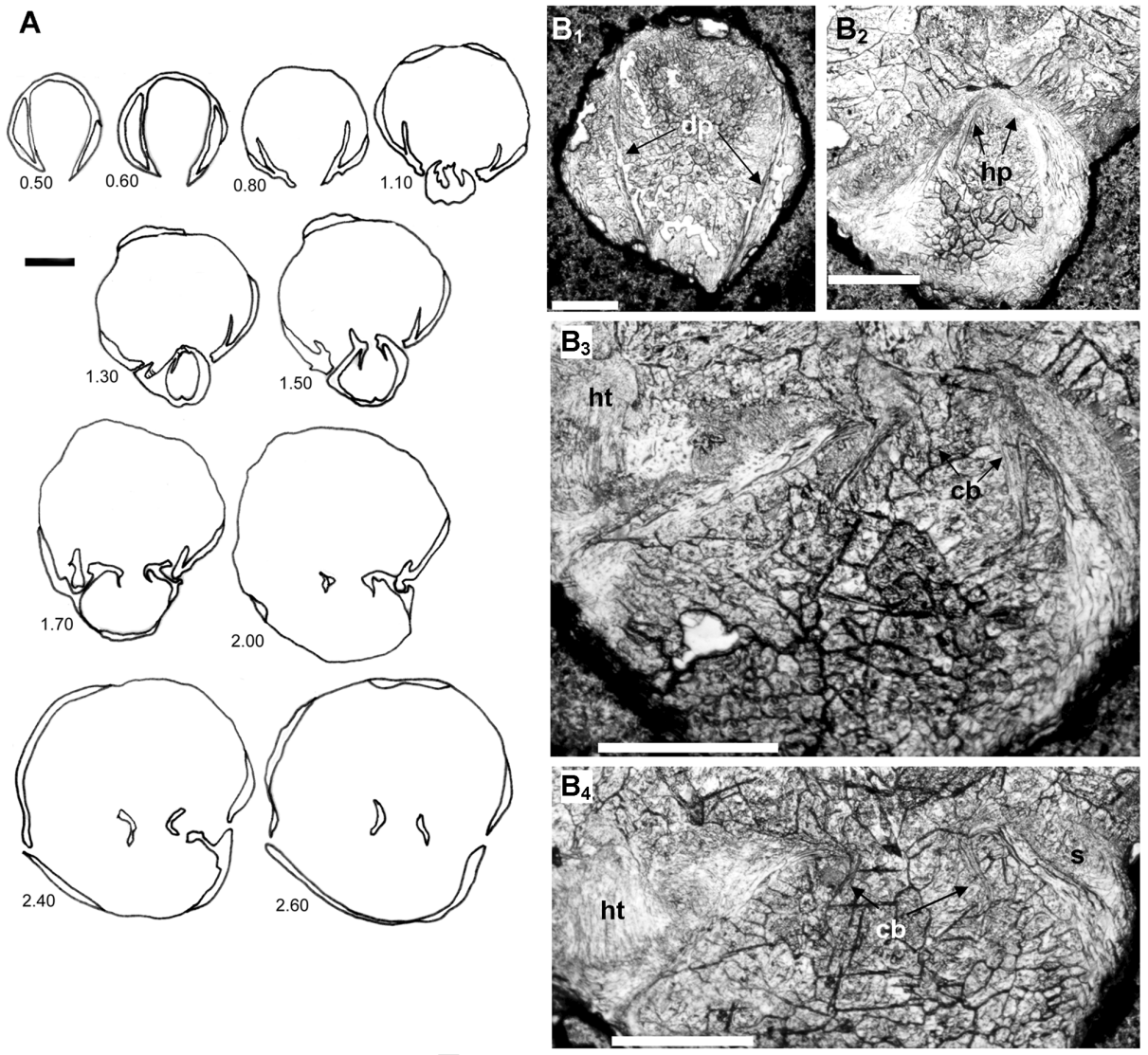

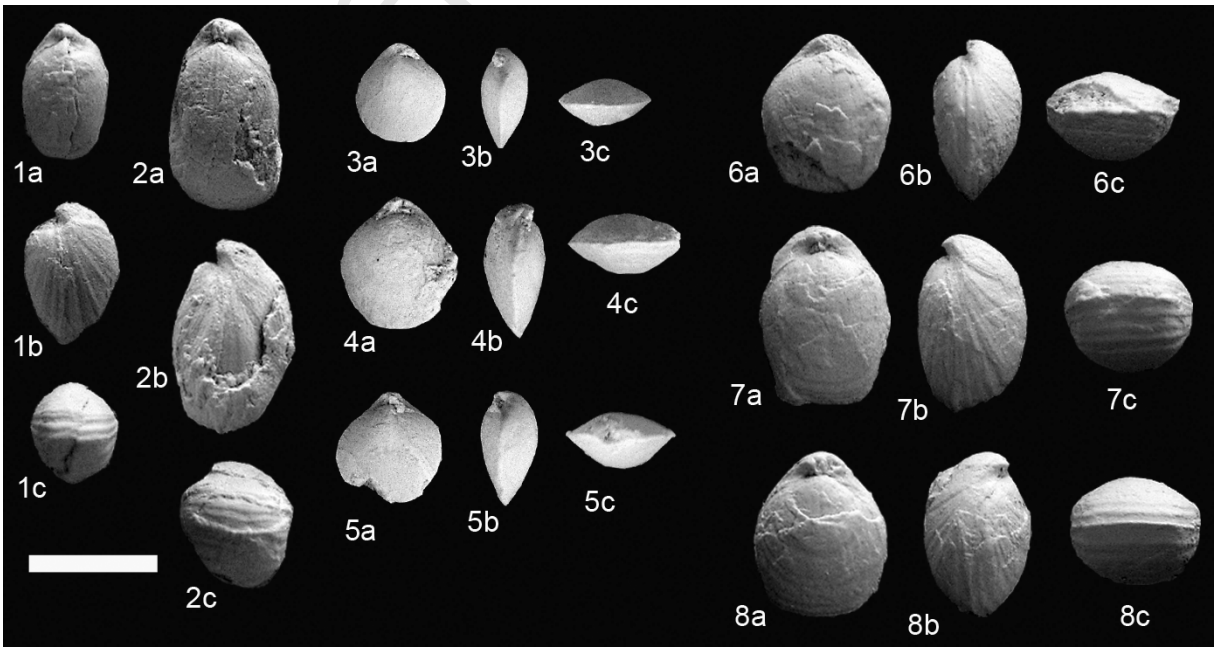

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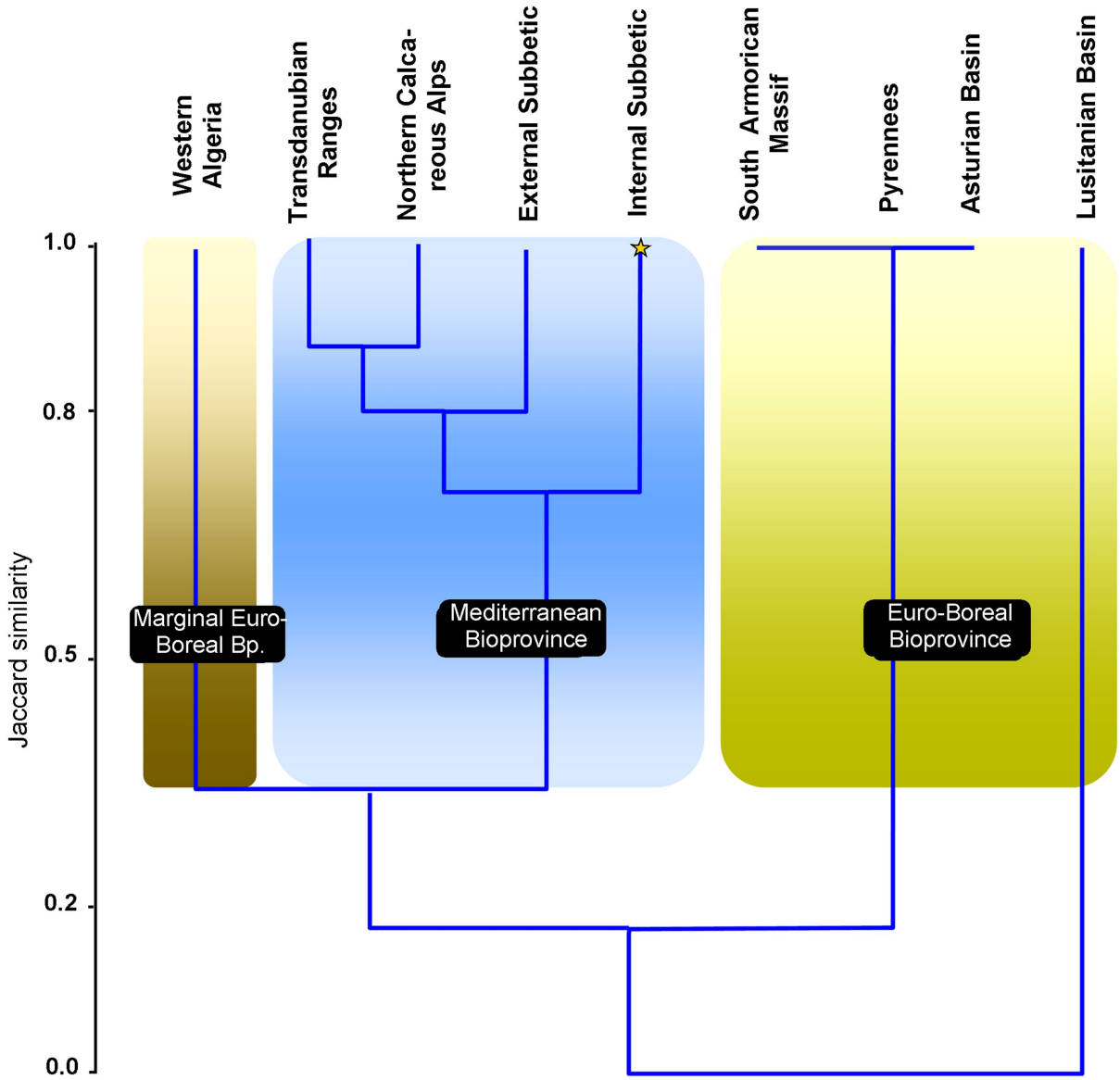

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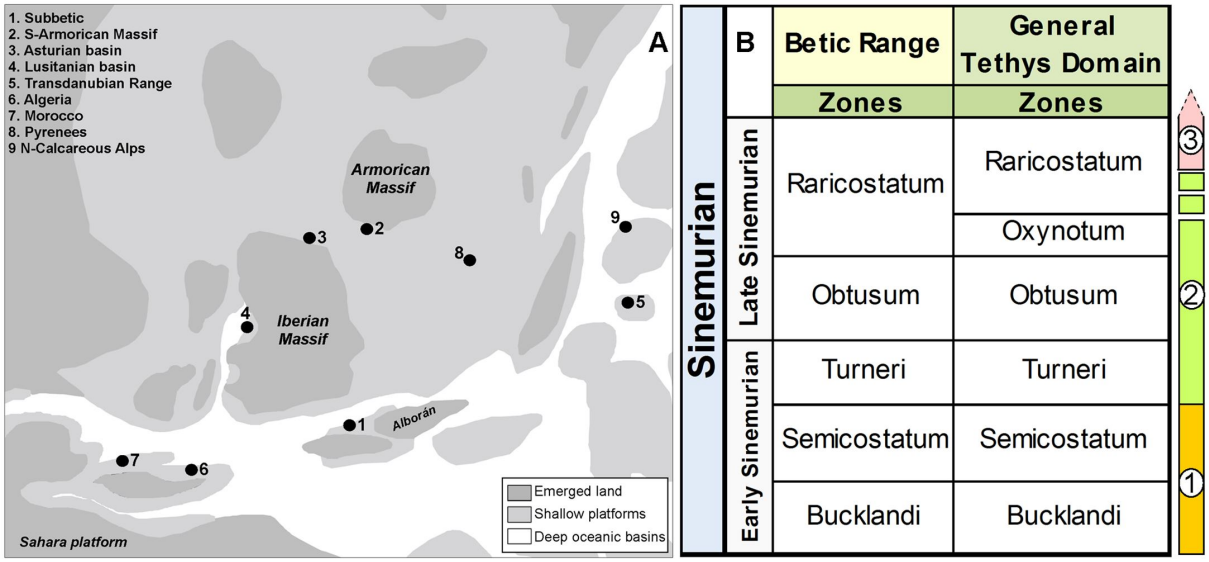

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