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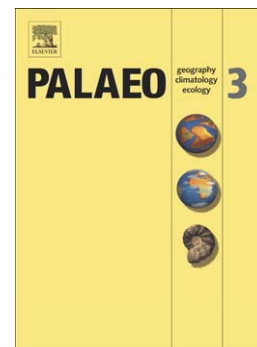
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Evolution of the last koninckinids (Athyridida, Koninckinidae), a precursor signal of the early Toarcian mass extinction event in the Western Tethys

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## ABSTRACT

Koninckinids are a suitable group to shed light on the biotic crisis suffered by brachiopod fauna in the Early Jurassic. Koninckinid fauna recorded in the late Pliensbachian–early Toarcian from the easternmost Subbetic basin is analyzed and identified as a precursor signal for one of the most conspicuous mass extinction events of the Phylum Brachiopoda, a multi-phased interval with episodes of changing environmental conditions, whose onset can be detected from the Elisa–Mirabile subzones up to the early Toarcian extinction boundary in the lowermost Serpentinum Zone (T-OAE). The koninckinid fauna had a previously well-established migration pattern from the intra-Tethyan to the NW-European basins but a first phase with a progressive warming episode in the Pliensbachian–Toarcian transition triggered a koninckinid fauna exodus from the eastern/central Tethys toward the westernmost Mediterranean margins. A second stage shows an adaptive response to more adverse conditions in the westernmost Tethyan margins and finally, an escape and

extinction phase is detected in the Atlantic areas from the mid-Polymorphum Zone onwards up to their global extinction in the lowermost Serpentinum Zone. This migration pattern is independent from the palaeogeographic bioprovinciality and is unrelated to a facies-controlled pattern. The anoxic/suboxic environmental conditions should only be considered as a minor factor of partial control since well-oxygenated habitats are noted in the intra-Tethyan basins and this factor is only noticeable in the second westward migratory stage (with dwarf taxa and oligotypical assemblages). The analysis of cold-seep proxies in the Subbetic deposits suggests a radiation that is independent of methane releases in the Subbetic basin.

**Keywords:** Early Jurassic, mass extinction, Koninckinids, Western Tethys.

## 1. Introduction

The well-known Early Toarcian Oceanic Anoxic Event (T-OAE) involved one of the most dramatic Mesozoic crises for the whole marine biota. Necto-planktonic communities and especially benthic ones were severely affected (e.g. Hallam, 1986, 1987; Little and Benton, 1995; Aberhan and Fürsich, 1997; Harries and Little, 1999; Vörös, 2002; Macchioni and Cecca, 2002; Wignall et al., 2005; Wignall and Bond, 2008; Caruthers et al., 2013; Arias, 2013; Reolid et al., 2014a). Brachiopods, in particular, revealed a very marked loss of diversity during this event (Vörös, 1993, 2002; Ruban, 2004, 2009; Vörös and Dulai, 2007; Baeza-Carratalá, 2013), actually disappearing from most of the basins for a long period. This event caused an entire faunal turnover (García Joral and Goy, 2000; Gahr, 2005; García Joral et al., 2011) and even marked post-event changes in the palaeobiogeographic pattern (Baeza-Carratalá et al., 2011; Baeza-Carratalá, 2013).

The orders Spiriferinida and Athyridida became extinct as effect of this event (Vörös, 2002; Comas-Rengifo et al., 2006). Koninckinids (Order Athyridida, Family Koninckinidae) are an unusual group among the Early Jurassic brachiopods and they are also very different from the remaining Mesozoic brachiopods, because of their minute size and peculiar shape that is very

similar to the Palaeozoic strophomenids. This group underwent an enigmatic and immediate radiation in the late Pliensbachian and then quickly became extinct in the early Toarcian (Vörös, 2002).

Koninckinid fauna has been widely recorded in the Western Tethys during the Pliensbachian–Toarcian transition, prior to the T-OAE (Gemmellaro, 1886; Steinmann, 1886; Rau, 1905; Manceñido, 1978; Alméras et al., 1988; Alméras and Elmi, 1993; Manceñido, 1993; Elmi et al., 1997, 2006; Sulser, 1999; Pozza and Bagaglia, 2001; Vörös, 2002, 2003; Comas-Rengifo et al., 2013). Mass-occurrences of koninckinids are well-known in the classical *Leptaena* beds and *Koninckella* faunas from England, Normandy, Portugal and Morocco, where they are often associated with typically dwarf or micromorphic assemblages. They have never been documented in the Betic Range, except for scarce citations in the works of Jiménez de Cisneros (1923, 1927).

Nowadays, copious specimens of koninckinids and of the usually associated fauna have been recorded and taxonomically analysed in several localities from the easternmost Subbetic area (Baeza-Carratalá, 2013). This finding enables correlations to be made and apparent relationships with the T-OAE to be inferred, as the first occurrence, radiation and sudden extinction of this fauna in this area took place in a short interval prior to the globally recorded definitive T-OAE.

Several probable causes of the early Toarcian mass extinction (global oceanic anoxic event vs. important warming episodes) and its possible diachroneity in the Western Tethyan basins are widely discussed (e.g. Jenkyns, 1985, 1988, 2003; Jenkyns and Clayton, 1986; Bassoullet and Baudin, 1994; Jenkyns et al., 1994; Jiménez et al., 1996; Harries and Little, 1999; Pálffy and Smith, 2000; Wignall et al., 2005; Mailliot et al., 2006; Zakharov et al., 2006; Gómez et al., 2008; Dera et al., 2010; Suan et al., 2010). Some previous authors have suggested that the mass extinction was really a multi-phased event (cf. Macchioni and Cecca, 2002; Wignall and Bond, 2008; Dera et al., 2010; Caruthers et al., 2013; cf. Arias, 2013) whose onset is detected early in the late Pliensbachian–earliest Toarcian times, with the main phase coinciding with the T-OAE as a result of a period of changes in long-term environmental conditions prior to this event (Dera et al., 2010;

Suan et al., 2010; García Joral et al., 2011). This major phase has been established, at least in the westernmost Tethys, within the Serpentinum Zone (Sandoval et al., 2012).

The easternmost Subbetic record of the koninckinid fauna allows the inference of a possible connection between the koninckinid records and these intervals prior to the extinction boundary. Therefore, their occurrence can be used as a precursor signal of the main crisis event within the possible multi-phased interval. In addition, the analysis of this fauna and related lithofacies attempts to provide new data on their relationship with episodes of anoxic and/or changing environmental conditions. In this sense, Subbetic faunas can be compared with analogous assemblages from well-oxygenated basins and also with those where they derived from black shales. The latter correspond to the classical *Leptaena* beds from the NW-European platforms and would represent anoxic/suboxic bottoms.

This approach is intended to provide new data not only on their relationship with the anoxia, but also about whether their radiation responds to a facies-controlled pattern. The palaeogeographical analysis also tests whether koninckinid occurrences in the Subbetic area fits in the distribution pattern detected by Vörös (2002) in the remaining western Tethyan basins, which shows E–W route dispersion from deeper intra-Tethyan basins to the relatively shallower NW-European areas.

Finally, Vörös (2002) linked koninckinid occurrences with hydrocarbon-seeps and a chemosynthesis-based way of life due to the remarkable correlation between koninckinid blooms and feasible cold-seep events. A tentative analysis of the Subbetic koninckinid-bearing deposits focused on cold-seeps proxies has been carried out, as the tectono-sedimentary framework of the Subbetic basin could be a priori propitious to lodging such cold-seeps (*sensu* Vörös, 2002; cf. Campbell et al., 2002; cf. Peckmann and Thiel, 2004) and an event of destabilization of marine gas hydrates just occurred during the Pliensbachian-Toarcian transition (Hesselbo et al., 2000, 2007; Vörös, 2002; among others). This analysis put forward a first overview for testing the methane-dependence hypothesis in this area, therefore contributing to a better understanding of the distribution pattern of this group.

## 2. Materials and Methods

Amidst the profuse Early Jurassic brachiopod fauna recorded in the Subbetic basin (Baeza-Carratalá, 2008, 2013), around 450 specimens belong to koninckinids and 54 to the usually associated *Nannirhynchia*. Specimens were collected from three localities (Fig. 1) together with the associate fauna determined and summarized in Fig. 2. They were complemented, after a systematic revision (Baeza-Carratalá, 2008), by taxa held in the Jiménez de Cisneros historical collection (JdC) deposited at the Palaeontological Museum of Murcia. Collected specimens are housed in the repository of the Earth and Environmental Sciences Department (DCTMA) at the University of Alicante (Spain).

The taxonomical assignments mainly follow recent works on systematic data in the Subbetic area and neighbouring Western Tethyan basins (e.g. García Joral and Goy, 2000; Baeza-Carratalá, 2008, 2011, 2013; Vörös, 2003, 2009; García Joral et al., 2011). The ammonite zonal/subzonal standard scheme used is according to Cariou and Hantzpergue (1997) and Aurell et al. (2002) for the Lower Jurassic of the Mediterranean Domain. Specific chronostratigraphical data for the Subbetic area (mainly from Braga, 1983; Iñesta, 1988; Caracuel et al., 2004; Sandoval et al., 2012) are also used.

In order to determine the possible presence of pyrite framboids and some other elemental proxies and, in turn, better characterize the koninckinid beds, microfacies and petrographical analyses of the most representative levels were undertaken using twelve selected thin sections and washed samples. Mineralogical composition of koninckinid-bearing levels was established by X-RD using a Bruker D8-Advance diffractometer (3000 W, 60 kV, 80 mA) in the Applied Petrology Laboratory of the University of Alicante through powdered samples. Thin section analyses also were performed under scanning electron microscopy (SEM; Hitachi S-300N) with energy dispersive X-ray spectrometry (EDS), obtaining an EDX Mapping, which provides element distribution and its relative proportion. Elemental geochemical analyses were also applied to bulk rock samples.

Outline curves enclosing isotopic data referred to the  $\delta C^{13}$  fluctuations from the Subbetic and Northern-Central Iberian margins are based on data from García Joral et al. (2011) and Sandoval et

al. (2012) and have been redrawn after the latter. These enveloping curves with the main values and deviations were correlated with brachiopod fauna bioevents and relative palaeotemperature variations from the central and northern marginal Iberian platforms (cf. García Joral et al., 2011).

### 3. Geological setting

Koninckinid faunas of the easternmost Subbetic area were collected from three outcrops located in the province of Alicante (SE Spain), forming part of the easternmost External Zone of the Betic Cordillera (Fig. 1). This region was situated in the South Iberian Palaeomargin (westernmost Tethys Ocean) in the Early Jurassic and was characterized by the predominance of shallow carbonate platforms, followed by more pelagic facies and epiocceanic swells and semi-grabens during most of the Jurassic and Early Cretaceous (Vera et al., 2004).

Koninckinid-bearing levels derive from the upper member of the Gavilán Formation (Van Veen, 1969) and the basal part of the Zegrí Formation (Molina, 1987). The first one mainly consists of crinoidal red glauconitic limestone beds with grainstone texture, and occasionally more calcarenite levels interspersed (Fig. 2). Apart from the crinoids, benthic foraminifers, abundant brachiopods, peloids and intraclasts are present. In the upper part, the strata show irregular tops with condensed pavements interpreted as hardgrounds with ammonoids, belemnites and brachiopods. Lenticular deposits of glauconitic sandy limestone with a dark greyish matrix containing brachiopods, ammonoids and gastropods are found overlying these pavements. In other cases, limestone with wackestone texture and phosphatized crusts can be found, revealing a stratigraphical unconformity formed before the onset of the marly sedimentation in the basin represented by the Zegrí Formation.

The Zegrí Formation starts at the base with alternating yellowish and greenish marls and marly limestone beds where mudstone texture predominates. These levels are set out in thin beds with irregular top and bottom surfaces. Levels of calcarenites and yellowish sandy marlstones containing koninckinids alternate sporadically. The marly sedimentation dominates upwards throughout the lower–middle Toarcian, indicating a pelagic depositional environment (Fig. 2).

#### 4. Koninckinid-beds from the Eastern Subbetic

##### 4.1. Koninckinid fauna

Koninckinid-bearing levels in the easternmost Subbetic are characterized by the mass occurrence of *Koninckella* and *Koninckodonta* genera (Fig. 3), which have been determined as six different species: *Koninckella bolivari* (Jiménez de Cisneros, 1927), *Koninckella gibbosula* (Gemmellaro, 1874), *Koninckodonta fornicata* (Canavari, 1883), *Koninckodonta* cf. *fornicata*, *Koninckodonta davidsoni* (Deslongchamps, 1853), and *Koninckodonta waehneri* (Bittner, 1894).

Both representatives of the *Koninckella* share most of their external features, such as smooth, small-sized shells with a narrow ventral sulcus, thus showing a slight anterior sinus, and straight cardinal edges. However, *K. gibbosula* has a subpentagonal dorsal outline, wider-expanded cardinal margin occasionally showing small postero-lateral wing-like extensions, the ventral valve is thinner and the beak is weaker. In contrast, *K. bolivari* is usually triangular in outline, with a highly incurved beak and sharp beak ridges; it has a very convex and thick ventral valve giving the shell a gryphaeoid appearance. *K. bolivari* was described and erected by Jiménez de Cisneros (1927) and can be considered as senior synonym of *Koninckella tiburtina* recorded from Tivoli by Vörös (2003).

The most profuse species among those assigned to the *Koninckodonta* is *K. fornicata*, thus distinguishing a subcircular large-sized *Koninckodonta* stock, wider than long, with straight posterior edges. *K. fornicata* shows a straight and large cardinal margin occupying more than half of the total width and a thin beak with a relatively large foramen, showing sharp beak ridges and wide and long interareas. The intraspecific variability of *K. fornicata* ranges from specimens with a stronger beak, shorter cardinal margin and nearly isometric shells to individuals showing shells wider than long, thinner beaks, and with the cardinal margin occupying 2/3 of the total width. Furthermore, *K. cf. fornicata* is herein suggested to point out those longer than wide shells with pronounced straight margins, developing a subpentagonal dorsal outline. *K. cf. fornicata* presents a



notable resemblance to *Koninckodonta styriaca* as figured by Bittner (1888) and Vörös (2003), but the intraspecific variability of this latter species remains to date unknown, hence the Subbetic material is prudentially regarded as a relative of *K. fornicata*.

In terms of abundance, the next *Koninckodonta* species recorded is *K. waehneri* (Bittner, 1894) quite similar to *K. fornicata*, but *K. waehneri* shows a pentagonal dorsal outline with rounded anterior margins, a flatter lateral view and straight postero-marginal flanks progressing until the mid-length, which are joined in the cardinal area developing an obtuse angle; the beak is less strong as well. Finally, *K. davidsoni* (Deslongchamps, 1853) is easily identifiable as being a large-sized and widening-expanded shell, commonly wing-shaped, with a subtrapezoidal to semicircular dorsal outline; the cardinal margin is straight and long, occupying nearly the total width of the shell.

#### 4.2. Associated assemblage in the koninckinid beds

The koninckinid fauna represents the most distinctive taxa of a wider assemblage from the latest Pliensbachian–earliest Toarcian (Assemblage 3 in Baeza-Carratalá, 2013) which typifies not only the first occurrence, bloom and sudden extinction of Koninckinidae, but also the acme of the *Nannirhynchia* and the *Orthotoma* unique finding in the easternmost Subbetic basin (Figs. 2, 4). In this way, species defined as being representative of the assemblage recorded in the koninckinid-bearing levels from the Subbetic area are *Nannirhynchia pillula*, *N. aff. gemellaroi*, *N. aff. reynesi*, *Orthotoma* sp., *Liospiriferina? undulata*, *Lobothyris arcta*, *Pseudogibbirhynchia? moorei*, *Quadratirhynchia crassimedia*, *Gibbirhynchia orsinii*, *Phymatothyris rheumatica*, and *Eplenythyris cerasulum*.

These distinctive taxa co-occur with species recurrently recorded in the Domerian, which are particularly abundant in these levels, such as *Securina oxygonia*, *Cirpa briseis*, *Salgirella alberti*, *Antiptychina? rothpletzi*, *Cisnerospira adscendens*, and *Lobothyris punctata*. Finally, an important stock of wider-range distribution taxa is recorded in these beds, mainly belonging to *Prionorhynchia*, *Viallithyris*, *Linguithyris*, *Liospiriferina*, and *Zeilleria*. The whole assemblage

shows a duality with regard to its palaeobiogeographical affinity (Iberian vs. Mediterranean). This coexistence of faunas in the Pliensbachian–Toarcian transition has also been noted in nearby basins such as the Iberian Range (García Joral and Goy, 2000).

Subbetic assemblages include the typical faunal components, at supraspecific level, recurrently recorded as constituents of koninckinid faunas from the Mediterranean areas from the Apennines and Bakony (Pozza and Bagaglia, 2001; Vörös, 2002, 2003) as well as from the classical British, German and Normandian *Leptaena* beds (Deslongchamps, 1853; Davidson, 1876; Rau, 1905; Ager, 1990), and *Koninckella* faunas recorded in France, Portugal and Morocco (Alméras et al., 1988; Alméras and Fauré, 1990; Alméras and Elmi, 1993; Elmi et al., 2006; Comas-Rengifo et al., 2013). However, at species level the Subbetic assemblages are quite different from the NW-European ones.

#### 4.3. Morphological pattern and taphonomical remarks in the Subbetic koninckinid beds

The Subbetic koninckinid beds include the distinctive minute koninckinid fauna associated with standard-sized taxa, therefore showing high taxonomic diversity (Fig. 2) without any prevailing morphological pattern. Together with the koninckinid fauna, large-sized, ribbed, and rectimarginate or uniplicate rhynchonellids (e.g. *Prionorhynchia*, *Cirpa*, *Salgirella*), which usually proliferate in habitats such as epioceanic swells, coexist with sulcate and smooth terebratulids (*Linguithyris*, *Viallithyris*, *Rhapidothyris*), sulcate zeillerids (*Bakonyithyris*) and axiniform morphotypes (*Securina*), a priori developed in deeper environments. Spiriferinids do not show a specific pattern either: a smooth subcircular *Liospiriferina*-type abounds, but many subpyramidal shapes (*Cisnerospira*) are also present, as well as strongly-ribbed forms (*Spiriferina muensteri*).

Conventionally minute forms as *Nannirhynchia*, *Orthotoma* and the koninckinid group itself are commonly regarded as inhabitants of oxygen-depleted or at least deeper habitats. However, the Subbetic individuals are far from representing a micromorphic assemblage. On the contrary, this fauna is made up of large-sized shells, since koninckinids reach the length of about 13 mm in some

*Koninckodonta* specimens and 7.2 mm in *Koninckella* individuals; moreover, *Nannirhynchia* specimens show a mean size of 9.7 mm in length and 10.1 mm in width, reaching up to 11.3 mm and 11.5 mm, respectively. Similar size patterns are recorded in Tivoli (Vörös, 2003), Bakony (Vörös, 2009) and Monte Serrone (Pozza and Bagaglia, 2001) and these latter authors emphasized the implications of such data. The opposite occurs in presumptive oxygen-depleted areas, such as Portugal, or North-African faunas where similar assemblages are recurrently dwarf or miniaturized. Thus, specimens of Portuguese *Koninckella* fauna from Rabaçal-Condeixa and Peniche have been directly examined for a comparison, with *Nannirhynchia* and koninckinids always being around 6 mm in length (Comas-Rengifo et al., 2013, 2015), and therefore a great deal smaller than the taxa in the Subbetic area.

Moreover, all the collected koninckinid specimens underwent taphonomic analysis, revealing that the fragile and minute shells are well-preserved. Shells are usually complete; tiny ornamentation as weak tubercles and growth lines are visible, pointing to minimal corrosion (Kolbe et al., 2011; Baeza-Carratalá et al., 2014). Articulated shells are dominant (nearly 99%), with a low degree of fragmentation and no perceptible blunt edges. The delicate features of the beak and cardinal area, such as minute foramen, beak ridges, hinge lines and wing-like expansions are often well-preserved. There are neither signs of bioerosion, encrustation, preferred orientation nor sorting. The shells commonly have their internal structure recrystallized and the shell infilling is usually the same as the host rock. All of these criteria probably point to moderate to negligible transport.

#### 4.4. Petrography of the Subbetic koninckinid-bearing levels

Koninckinid fauna derived from the red crinoidal limestone of the Gavilán Formation as well as from the calcareous sandy marlstone levels located in the basal parts of the Zegrí Formation. The red crinoidal limestone reveals a crinoidal packstone/grainstone microfacies with very rare benthic foraminifers and pellets (Fig. 5A–C). Both packing and sorting of bioclasts are very high; preferential orientation, micritization and bioerosion are absent. Porosity is extremely low and in

the scarce examples observed it is related to intergranular porosity. In those cases, a first rim of dog tooth calcitic cement is present all around the void, while the filling is represented by calcite blocky cement (Fig. 5A); no banded cement has been observed. In the very rare micritic patches, micrite is homogeneous and no sign of clotted microfabrics has been observed.

The microfacies of the calcareous sandy marlstone beds of the Zegrí Formation are represented by very fine-grained packstone/densely packed wackestone (Fig. 5D–F). Brachiopod shells, crinoids, thin-shelled bivalves and echinoids spines are recognizable. The matrix is scarce and homogeneous and no clotted distribution has been observed. Cements are completely absent. Although not observed at macroscopic scale, horizons with aligned bioclasts are visible in thin section. It is remarkable that these horizons are not iso-oriented to each other. Bioclasts are not micritized; abrasion and bioerosion have not been observed, but it could also be due to the very small size of the shells. Spots of oxides with diagenetic halo are present (Fig. 5D–F). SEM analysis confirmed their nature as iron oxides and excluded their derivation from the oxidation of previous sulphides (Fig. 5, 6).

The mineralogical composition of both facies is nearly equivalent. The peaks of X-RD analysis (Fig. 6) reveal that crinoidal red grainstone and calcareous sandy marlstone consist almost exclusively of carbonate represented by the calcite phase and only a minor amount of quartz is present in the samples of the Zegrí Formation (fig. 6A). Pyrite is totally absent. Elemental geochemical analysis reveals a high content in O, Ca, Si, Fe, Al, and Cl in all the samples, being Ba, Mg and K secondary elements; finally, elements such as S, Sr or Ti are represented with very low values (Table 1).

## **5. Biostratigraphical record of the koninckinid beds**

### *5.1. Age of the koninckinid-bearing beds in the easternmost Subbetic area*

Biostratigraphical markers like ammonoids are very scarce in the koninckinid-bearing beds and equivalent levels from the easternmost Subbetic area. The records of *Hildoceras* sp. and

*Harpoceras* sp., in the basal levels of the Zegrí Formation, were attributed to the lower Toarcian by Geyer in Azéma (1977). Likewise Tent-Manclús (2006) attributed to the lower Toarcian comparable levels from neighboring outcrops (El Cantón; Fig. 1) with *Hildaites* sp.

The koninckinid beds unequivocally overlie a ferruginous level in the Cerro de la Cruz section with *Calliphyloceras bicolae*, *Lytoceras villae*, *Protogrammoceras celebratum*, *Fuciniceras isseli*, and *Meneghiniceras lariense*, attributed to the upper Pliensbachian (Lavinianum Zone, Cornacaldense Subzone) and underlie a hardground with *Dactylioceras* sp., *Protogrammoceras bassanii*, *Nodicoeloceras*, *Catacoeloceras*, *Osperleioceras*, *Phymatoceras*, *Pseudolillia*, *Hildoceras*, *Catullocceras*, and *Graphoceras* gr. *concaum*, therefore including chronorecords from the lower Toarcian to the Aalenian (Iñesta, 1988; Caracuel et al., 2004).

In the Tarabillo and Sierra de Orts sections (Fig. 2), condensed levels with *Fuciniceras portisi*, *F. lavinianum* and *F. isseli* underlie the koninckinid beds. These levels were attributed to the basal upper Pliensbachian (Lavinianum Zone, Portisi Subzone) by Braga (1983) and Baeza-Carratalá (2013). In addition, koninckinids in these outcrops are recorded together with some constituents of a brachiopod assemblage (e.g. *Liospiriferina? undulata* and *Lobothyris arcta*) whose biostratigraphical range is mostly restricted to the Tenuicostatum Zone in the nearby Iberian basin (Goy et al., 1997; García Joral and Goy, 2000; Comas-Rengifo et al., 2006; García Joral et al., 2011).

Calcareous nannoplankton analysis shows that koninckinid fauna is recorded in the Sierra de Orts section together with *Lotharingius hauffii*; in the Cerro de La Cruz section just below a level with *Orthogonoides hamiltoniae*, *Lotharingius* sp., and *Parhabdolitus* sp. Likewise, some constituents of the koninckinid beds have been recorded in La Algueda section (Fig. 1) together with *Lotharingius* sp. (C. Lancis, 2008, pers. comm.).

First occurrence (FO) of *L. hauffii* is used for the definition of the NJT5 CNZ established by Mattioli and Erba (1999). In the Iberian platforms, this species shows the FO in the Basque-Cantabrian and Asturian basins in the lowermost Margaritatus Zone (Perilli et al., 2010; Fraguas

and Young, 2011). However, Mattioli et al. (2013) recently settled the FO of *L. hauffii* in the NJ5a within the Emaciatum Zone from the Lusitanian basin. These authors explained that the FO of *L. hauffii* is located within the Margaritatus Zone in NW Europe, but in Italy and the Lusitanian basin it took place within the Spinatum Zone. On the other hand this event occurs within the Emaciatum Zone in the Tethyan Domain (Mattioli and Erba, 1999). Reggianni et al. (2010) also placed this event in the Solare Subzone in Peniche. Sandoval et al. (2012) recorded the joint occurrence of *L. hauffii* together with *Orthogonoides hamiltonae* in the NJT5b CNZ, in the Solare–Mirabile subzones interval in the Subbetic area.

All these biostratigraphical data led to dating the koninckinid beds in the uppermost Pliensbachian–lowermost Toarcian (Spinatum–Polymorphum zones), just prior to the faunal crisis related to the T-OAE, which took place in the lower part of the Serpentinum Zone (Levisoni Subzone) in the Median Subbetic (Sandoval et al., 2012), just as in Portugal, where Comas-Rengifo et al. (2013) set the extinction level in the Elegantulum Subzone (Serpentinum Zone).

## 5.2. Comparison with koninckinid records from Mediterranean areas

The record of index bioevents generally identified in the koninckinid beds (e.g. koninckinid and *Nannirhynchia* acmes) are not usually associated either to the oxygen-depleted environments or black shale deposits in the more intra-Tethyan Mediterranean basins. Correlating the Subbetic assemblage with those recorded in Mediterranean areas, the best relationship seems to be found in the koninckinid levels reported in the Apennines, both in Tivoli (Vörös, 2003) and Monte Serrone (Pozza and Bagaglia, 2001).

Koninckinid faunas from Tivoli are recorded within nodular crinoidal limestone with marly matrix beds, outcropping between the Corniola Formation and the overlying marly Monte Serrone Formation. The Tivoli assemblage shares very close related taxa with the Subbetic one (*Koninckella bolivari*, *K. gibbosula*, *Koninckodonta fornicata*, *K. waehneri*, *K. davidsoni*, *K. styriaca* (?), *Nannirhynchia reynesi*, *N. gemmellaroi*, *Gibbirhynchia* cf. *orsinii*, *Cirpa briseis*, *Linguithyris*

*aspasia*, *Antiptychina? rothpletzi*, and *Liospiriferina alpina*). This assemblage was tentatively assigned to the earliest Toarcian by Vörös (2003), pointing out a possible Pliensbachian–Toarcian mixing either due to the major persistence of the Corniola Formation in Tivoli rather than in other areas of the basin, or arguing a redeposition of Pliensbachian sediments into the lower Toarcian. In any case, Vörös (2002) considered the latest Pliensbachian–earliest Toarcian as a remarkable interval when a koninckinid diversity flourishment took place in Apennines and Sicilia that then abruptly became extinct due to the T-OAE. A comparable situation occurs in our studied outcrops, and therefore some connecting links can be inferred.

Other comparable *Koninckella* fauna unconnected to black shales was recorded in Umbria by Pozza and Bagaglia (2001). These authors described an assemblage from Monte Serrone that is slightly different from that studied here, but with quite similar morphotypes, sizes and depositional conditions. The most significant species defined in these levels are, among others, *K. gibbosula*, *K. liasiana*, *N. pygmaea*, *Phymatothyris rheumatica*, *Eplenythyris cerasulum*, *Linguithyris aspasia*, and *Ortothoma apenninica*. This assemblage is assigned to the lower Toarcian (Polymorphum Zone). Subsequent studies (Bilotta et al., 2010) specified the age of this *Koninckella* fauna levels in the lower part of the Semicelatum Subzone = mid-Polymorphum Zone on the standard Tethyan ammonite zonation. The similarity with the Subbetic assemblage is heightened if we consider that *N. pygmaea* and *K. liasiana* depicted by Pozza and Bagaglia (2001) are far from being the typical forms of these taxa as they are known in the western basins, with *N. pygmaea* being very close to the Subbetic *N. aff. reynesi*. A similar situation can be argued for the Swabian specimens of *K. liasiana* figured by Rau (1905) from the Spinatum Zone, with a subcircular outline, very close to the *K. gibbosula*-type. Possibly this specimens, as well as the recorded by Steinmann (1886) in Thuringia, are different of the typical *K. liasiana* from the Western basins.

Principi (1910) also reported a diverse fauna from Umbria assigned to the “middle Liassic” in which several species attributable to *K. fornicata*, *N. reynesi*, *Cirpa briseis*, *Lobothyris punctata*,

*Linguithyris aspasia*, *Salgirella alberti*, *Eplenythyris cerasulum*, *Phymatothyris rheumatica*, and *Securina oxygonia* can be found. All of these taxa are also present in the Subbetic assemblages.

Concerning the possible equivalence with the Hungarian koninckinid faunas, the resemblance between Transdanubian Early Jurassic brachiopod assemblages and the Subbetic ones is well-known (see e.g. Vörös, 1993, 2009; Baeza-Carratalá, 2013). This similarity, plainly evident in the associated taxa, is also extensive to the record of *Nannirhynchia* + koninckinids bloom (Vörös, 2002), with the Subbetic *Nannirhynchia* forms being close to the Hungarian *N. gemmellaroi* and *N. reynesi*, and also sharing very closely related forms to the Hungarian *Koninckodonta* cf. *waehneri*, although the Hungarian records are assigned to the Margaritatus Zone (Vörös, 2002).

Other representative faunas in the Pliensbachian–Toarcian transition were recorded from Sicily (Gemmellaro, 1886) with several “*Leptaena*” species as *L. davidsoni* or *L. gibbosula*, and from Western Greece (Renz, 1932; Manceñido, 1993), but they only share *K. fornicata* with the Subbetic material (specimens formerly attributed by Renz to *R. aff. reynesi* were tentatively updated as belonging to *Cuneirhynchia* and *Cirpa* by Manceñido, 1993).

### 5.3. Comparison with koninckinid records from NW-European platforms

In his exhaustive analysis of the koninckinid distribution pattern, Vörös (2002) draws attention to the dating of the classical *Koninckella* fauna from Normandy, Portugal and Morocco, setting them in the upper Tenuicostatum Zone (Semicelatum Subzone) and to the typical British *Leptaena* beds, most of which are usually linked to black shale deposits. On the contrary, the *a priori* older Subbetic koninckinid fauna is recorded in red crinoidal limestone and in sandy marlstone beds denoting the onset of marly sedimentation.

The classical British localities where the *Leptaena* beds (e.g. Davidson, 1876; Ager, 1990) and their equivalent French *Koninckella* fauna (e.g. Deslongchamps, 1853; Alméras et al., 1988; Alméras and Elmi, 1993; Elmi et al., 1997) were recorded are mainly attributed round the Tenuicostatum–Falciferum zonal boundary, some British records even reaching the lower part of



the Serpentinum Zone (Vörös, 2002). These beds are distinguished by the occurrence, among others, of *Nannirhynchia* (mainly *N. pygmaea*), koninckinids (*Koninckodonta davidsoni*, *Koninckella bouchardii*), and *Orthothoma globulina*. Similarly, Alméras et al. (1991) considered the co-occurrence of *N. pygmaea* + *K. bouchardii* as subzonal biostratigraphical markers equivalent to the Semicelatum Subzone.

Likewise, Alméras et al. (1988) reported an early Toarcian *Koninckella* fauna in Portugal and the North-African platforms (within the basal Polymorphum Zone), comprising among others *Koninckella liasiana*, *N. pygmaea*, *Pseudokingena deslongchampsii*, and *Pseudogibbirhynchia moorei*, coeval with Dimerian foraminifera. Elmi et al. (2006) and Alméras et al. (2007) recorded a *Koninckella* fauna made up of *N. pygmaea*, *K. liasiana* and *Cadomella* cf. *moorei* from the uppermost Pliensbachian (Emaciatum Zone, Elisa–Solare subzones) to the lowermost Toarcian (Polymorphum Zone, Mirabile Subzone) in NW-Algeria. Together with these representative taxa, specimens of *P. kerkyraea*, *Lobothyris punctata* and *Quadratirhynchia quadrata* were also recorded in the Elisa–Solare subzones and *Liospiriferina subquadrata* and *Lobothyris* sp. in the Mirabile Subzone. All of them can be regarded as similar morphotypes to those recorded in the Subbetic assemblages (e.g. *P. rheumatica*, *Lobothyris arcta*, *L. punctata*, *Liospiriferina?* *undulata*).

Recently, equivalent records and morphotypes were also reported by Comas-Rengifo et al. (2013, 2015) in the Lusitanian basin with a *Koninckella* fauna composed of *N. pygmaea*, *K. liasiana*, *Pseudokingena deslongchampsii* together with *Liospiriferina?* aff. *undulata*, *L. subquadrata*, and representatives of *Cisnerospira*, *Zeilleria*, *Cirpa*, and *Gibbirhynchia* recorded in the Polymorphum Zone and in the basal beds of the Levisoni Zone (levels with *Eleganticeras elegantulum*).

This comparative analysis of Subbetic vs. NW-European faunal content shows some similarities at supraspecific level both in the koninckinid fauna *sensu stricto* and morphotypes, and in the usually associated taxa. In spite of this, substantial differences at species level have been evidenced between the classical *Koninckella* faunas from the North-African/Atlantic platforms and the

Subbetic assemblages, with the dwarf taxa being the prevailing fauna in the koninckinid beds commonly associated to oxygen-depleted areas. As for their age, the Subbetic assemblages are close to the North-African ones, being somewhat younger (exclusively Toarcian) in Portugal, England and France.

## 6. Discussion

### 6.1. Depositional environment of the Subbetic koninckinid beds

The palaeoenvironmental evolution of the easternmost Subbetic area in the Early Jurassic is comparable to the majority of the perimediterranean Tethyan palaeomargins. It took place in an extensional tectonic framework related to the Tethyan rifting that evolved from shallow carbonate platforms to an epioceanic swell/trough system. The platform drowning led by listric faults alternated deepening-infilling episodes in this system during the Pliensbachian and originated some extensional fractures and crevices in the epioceanic escarpments (Tent-Manclús, 2006). In a posterior phase, the lack of activity of the listric faults facilitated generalized infilling of the irregularities of the sea bottom.

This depositional scenario fits with the evolutionary model proposed for koninckinids (Vörös, 1986, 2002). According to this model, in the Pliensbachian, koninckinids preferred inhabiting the crevices developed in the escarpments of the epioceanic swells and only later colonized soft muddy bottoms. In the Subbetic basin the context was made more favorable by the fact that the extensional fractures offered empty niches to be colonized by koninckinids and *Nannirhynchia*, among others, in their E–W Tethyan migration route.

The high taxonomical diversity and abundance of specimens found in the koninckinid beds would suggest a hypothetical mixing of taxa, with transport affecting species from different niches. It could be also supported by the pseudolobular disposition in the prograding crinoidal grainstone beds and the significant lateral changes in thickness and bedding (Fig. 2). This setting suitably fits a depositional scenario associated with minor grainflow deposits (cf. Vörös, 1986, 1994; Jach, 2005;

Baeza-Carratalá, 2013) that accumulated sediments in a transitional seamount-depression environment. However, the coexistence of minute and standard-sized taxa cannot be considered as an indication of important remobilisation, since it is a common feature not exclusive to the Subbetic area. In fact, this coexistence was also previously noted in some other intra-Tethyan basins with potentially correlatable assemblages (e.g. Vörös, 2003) and also in the younger typical NW-European *Koninckella* faunas. These are conventionally characterized by dwarf assemblages where dominant micromorphic *Koninckella* and *Nannirhynchia* are usually recorded together with standard-sized spiriferinids and rhynchonellids regarded as of Dimerian condition (Almérás et al., 1988; Almérás and Elmi, 1993), as found in the Subbetic beds.

In addition, taphonomic evidences point to negligible transport, so that the associations may be considered as local parautochthonous assemblages, with both source and depositional areas being in close proximity. It is even feasible that the koninckinid fauna may have remained in its original habitat.

#### 6.2. Facies and anoxia control in the Subbetic koninckinids

The rapid and enigmatic radiation of the latest Pliensbachian–early Toarcian koninckinids and its peculiar morphological pattern was explained by Vörös (2002, 2003) partly as an adaptation to inhabit soft bottoms or muddy substrates, giving rise to the well-known gryphaeoid and flat-lying morphotypes, both being functional for this purpose. In most of the Mediterranean and European localities, koninckinids are related to soft, muddy substrates and even to black shales. However, in the Subbetic occurrences, both aforesaid morphotypes coexisted together with the more subelliptical ones (e.g. *K. bolivari*, *K. fornicata* and *K. davidsoni* coexisting together) in the sand-grained substrates represented by the red crinoidal limestone of the Gavilán Formation and the sandy marlstone of the Zegrí Formation. Therefore substrate consistency cannot be considered a limiting factor for koninckinids distribution and the same morphological adaptations to muddy bottoms were retained in the colonization of sandy substrates. Thus, the morphological adaptive response

observed in the easternmost Tethyan areas (Vörös, 2002) could be functional in generally unconsolidated sediments rather than only in muddy bottoms, at least in the eastern Subbetic area.

On the other hand, easternmost Subbetic occurrences are not linked to a potential anoxia-controlled distribution of the koninckinids, as could be inferred from their profusion in several NW-European localities where koninckinids and *Nannirhynchia* are associated to anoxic/dysoxic environments. In all the sections herein studied (Fig. 2), koninckinid faunas were recorded in sediments without any sign of reductive conditions. Both crinoidal limestone and calcareous sandy marlstone beds represent environments with a well-developed benthic community, productive in suspension- and filter-feeder biota. The crinoidal limestone clearly represents a sandy bioclastic winnowed substrate, characterized by a quite low sedimentation rate, most probably related to the presence of steady currents. In both facies, the absence of pyrite and organic-rich horizons as well as the abundance of remains of benthic organisms indicate normal oxygen supply conditions of the seafloor. This can be also corroborated by the main biometric indices analyzed in the Subbetic koninckinid fauna, which can be regarded as mature communities with large-sized shells (even larger than the mean size found in other Mediterranean basins).

Close similarities have been observed in terms of both fauna and depositional environment with the type section of the Monte Serrone Marls Formation (lower Toarcian), represented by yellowish marls without any trace of pyrite and interbedded silt levels (Pozza and Bagaglia, 2001), these authors emphasizing the normal environmental conditions recorded in the section. The same comparable size pattern is seen in other epiocenic areas like Tivoli (Vörös, 2003) or Bakony (Vörös, 2009).

Conversely, in several NW-European localities, koninckinids and *Nannirhynchia* are recurrently represented by dwarf assemblages associated with anoxic/dysoxic environments and even black shales (e.g. Portugal, England, and Normandy). In fact, the very small size is clear evidence of adverse ecological conditions, preventing organisms from reaching a standard size. In these oxygen-depleted platforms, koninckinid faunas are usually recorded together with remains of pyrite (e.g.

Alm eras et al., 1988; cf. Wignall and Bond, 2008), usually present as framboidal growth. An attempt to detect pyrite and framboidal growths has been made in the Subbetic levels (Figs. 5G–H, 6; Table 1), but pyrite resulted absolutely absent.

Hence, association with black shale or oxygen-depleted environments is not a rule for the occurrence of the koninckinid fauna, but should only be considered as a factor of partial influence. It is noteworthy that where oxygen-supply conditions appear to have been around normal values, koninckinids are larger than the miniaturized fauna described for the NW-European localities (except for *K. davidsoni*, which keeps indiscriminately its large size).

### 6.3. Implications of the Subbetic assemblages in koninckinid fauna distribution

In the Western Tethys, V r s (2002) ascertained that the palaeogeographical dispersion route of the koninckinids evidences a marked E–W migration from the intra-Tethyan areas to the epicontinental relatively shallow muddy platforms. The taxonomical content, biostratigraphical data, and depositional conditions analyzed in the Subbetic koninckinid fauna allow its inclusion in this migration route (Fig. 7), highly influenced by the prevalent oceanic current pattern. In this route, the perimarginal areas of Iberia, including the Subbetic basin, played a significant role linking the epioceanic-epicontinental habitats either via the Lusitanian Basin or via the Laurasian Seaway (*sensu* Bjerrum et al., 2001; V r s, 2002).

In this sense, the easternmost Subbetic basin was the westernmost Tethyan area where the koninckinid fauna is recorded in a clearly oxygen-rich epioceanic environment from the latest Pliensbachian–earliest Toarcian (Fig. 7). The following westward koninckinid fauna in this longitudinal pathway is recorded in the North-African basins (Elmi et al., 2006; Alm eras et al., 2007), also in the upper Pliensbachian–lower Toarcian (Elisa–Mirabile zones) but with different species associated with organic-rich facies. Then, the following step in this route towards the Atlantic areas is the Lusitanian basin, clearly early Toarcian in age, with the koninckinid fauna being recorded in organic-rich facies and muddy bottoms.

The Subbetic koninckinid fauna consequently completes the pattern turning around Iberia, linking the upper Pliensbachian-lowermost Toarcian records from the Apennines and other easternmost Tethyan regions with the NW-European Toarcian records. It is also predictable that this dispersal route led through the westernmost areas of the Subbetic basin, as the Median Subbetic hemipelagic trough is a sea-arm connected with the Hispanic Corridor (Sandoval et al., 2012; cf. Rodríguez-Tovar and Reolid, 2013), probably also promoting migration through the Atlantic seaway.

This intra-Tethyan/Atlantic transition is conducted by conventional-sized vs. dwarf faunas, giving rise to a taxonomical replacement. Thus, e.g. the stock of *Nannirhynchia reynesi*, *N. gemmellaroi*, *N. pilulla* and related forms recorded in epioceanic environments is replaced in the NW-European areas by miniaturized assemblages, where *Nannirhynchia* become monospecific (*N. pygmaea*) and a turnover in the koninckinid species is noticed (dominance of *K. liasiana* and *Koninckodonta davidsoni* in the Atlantic basins). In addition, the supraspecific taxonomical attributions recorded in the koninckinid fauna (*Nannirhynchia*, *Koninckella*, *Koninckodonta*, *Orthotoma*) seems to be consistent in the Western Tethys as a whole, better fulfilling a mere species renewal in the Atlantic basins. Accordingly, a radiation independent from the palaeobiogeographical provinciality can be deduced.

#### 6.4. Latest koninckinid evolution as precursor signals of the T-OAE

Among the several topics related with the T-OAE, it remains unsolved whether this mass extinction better responds to a single and restricted phase or is a consequence of continuous changes in a wider interval. It is widely suggested that the early Toarcian mass extinction was really a multi-phased event (cf. Macchioni and Cecca, 2002; Kemp et al., 2005; Wignall and Bond, 2008; Dera et al., 2010; Caruthers et al., 2013; cf. Arias, 2013) whose onset is detected in the late Pliensbachian-earliest Toarcian times, with the main extinction phase coinciding with the T-OAE as a result of long-term changes in environmental conditions prior to this event (e.g. Dera et al., 2010; Suan et al.,

2010; cf. García Joral et al., 2011). The extinction boundary has been established, at least in the westernmost Tethys, within the Serpentinum Zone (Sandoval et al., 2012; Comas-Rengifo et al., 2013, among others).

A current research trend justifies the alteration of environmental conditions in the pre-T-OAE interval in terms of oscillation of seawater temperatures, mainly deduced from isotopic data referred to the  $\delta C^{13}$  and  $\delta O^{18}$  fluctuations, often correlated with manifest bioevents. Palaeotemperatures from Western Tethys in the late Pliensbachian indicate a remarkable cooling interval (Bailey et al., 2003; Rosales et al., 2004; Gómez et al., 2008; Suan et al., 2010; García Joral et al., 2011; Harazim et al., 2013; Metodiev et al., 2014) followed by the onset of a progressively warmer episode coinciding with the early Toarcian. This lasted up to the uppermost Tenuicostatum–lower part of the Serpentinum zones, when a notable sudden increase in temperature occurred, holding the foremost extinction boundary (Gómez and Goy, 2011; García Joral et al., 2011; Harazim et al., 2013).

Early research on the T-OAE in the Subbetic basin (Jiménez et al., 1996; Jiménez and Rivas, 2007) indicated several excursion pulses in the  $\delta C^{13}$  and  $\delta O^{18}$  values connected with biotic events in the Polymorphum–Serpentinum interval. Such studies also deduced significant palaeotemperature variations, mainly referred to a sudden increase in the Serpentinum Zone related to the extinction boundary, but also detecting previous episodes of Mediterranean/Boreal faunal temperature-controlled exchanges, in a similar way to other basins (Cecca and Macchioni, 2004).

Recently, Sandoval et al. (2012) revealed several  $\delta C^{13}$  and  $\delta O^{18}$  fluctuations correlated with ammonite and nannoplankton turnovers in this area, from the latest Pliensbachian up to the definitive peak related to the main Serpentinum Zone (Levisoni Subzone) event. Prior to this peak, Sandoval et al. (2012) recorded bioevents coinciding with isotopic variations within the Elisa, Mirabile and Semicelatum (several peaks/bioevents) zones. These authors performed a very comprehensive comparative analysis of geochemical fluctuations/turnovers in most of the Western Tethyan basins, recognizing a similar pattern (with slight variations, as expected) in Northern and

Central Spain, Portugal, Southern Alps, Apennines, Hungary, Greece, and the French and British basins.

The easternmost Subbetic koninckinid fauna is recorded in correspondence with the onset of these environmental changes in the latest Pliensbachian–early Toarcian. This allowed the connection of the koninckinid records with the intervals preceding the extinction acme in the Serpentinum event (Fig. 8), so that their occurrences can be used as precursor signal of this main crisis event within this possible multi-phased interval.

Bearing in mind the predominant current pattern estimated by Bjerrum et al. (2001) and the latitudinal control on the brachiopod distribution put forward by García Joral et al. (2011), a first cooling episode or, at least, favorable lower temperature conditions can be deduced through the brachiopod fauna in the Subbetic area. Thus, prolific brachiopod assemblages are widely recorded up to the latest Pliensbachian (Baeza-Carratalá, 2013). In the succeeding episode, a progressive warming leads to the coexistence of distinct assemblages in the late Pliensbachian–earliest Toarcian, evidencing the progressive replacement by species better adapted to warmer environments like *Lobothyris arcta* or *Liospiriferina undulata* (*sensu* García Joral et al., 2011; Baeza-Carratalá, 2013). Koninckinid faunas are also recorded in these levels revealing the stage of their westward migration route, from the East-Mid Mediterranean areas (Greece, Apennines, Bakony; cf. Manceñido, 1993; Vörös, 2003, 2009) towards the Western Tethys regions (Vörös, 2002). They found a suitable habitat to colonize in the easternmost Subbetic (*sensu* Vörös, 2002), dominated by epioceanic platforms with extensional fractures and crevices.

Afterwards, koninckinids adapted to new environmental conditions. The last occurrence of Mediterranean-type koninckinid fauna in the Subbetic hence typifies the onset of the progressive warming episode prior to the T-OAE, being indicative of these changing conditions in the westernmost Mediterranean areas in the Elisa–Mirabile? subzones, corresponding to the isotopic anomalies detected by Sandoval et al. (2012) (Fig. 8).



The next stage in the westward koninckinid migratory route reaches the North-African and NW-European platforms (Vörös, 2002, Elmi et al., 2006). This migratory event is linked to a notable reduction in size and diversity, affecting not only koninckinids, but also associated genera such as *Nannirhynchia*, representing a replacement conducted by conventional-size vs. dwarfism. As previously mentioned, the stock of *Nannirhynchia reynesi*, *N. gemmellaroi*, *N. pilulla* and related forms recorded in Mediterranean and well-oxygenated environments is replaced by miniaturized and oligospecific assemblages with *N. pygmaea* due to more adverse environmental conditions (adaptive turnover in Atlantic basins in Fig. 8). A similar turnover (with reduction in size and diversity) is noticed in the koninckinid species (dominance of the minute *Koninckella liasiana* with only scarce large-sized *Koninckodonta davidsoni*). Contrary to the long-established schema which typically related koninckinid fauna with low oxygen-supply, the large koninckinids adapted their morphology to these conditions evolving to miniaturized species only from this phase onwards, as several other groups did (cf. García Joral et al., 2011).

While this evolutionary turnover was taking place in the westernmost margins, some intra-Tethyan zones like Umbria played a role as a relict area where the former diverse and numerous koninckinid fauna persisted up to the mid-Polymorphum Zone (Pozza and Bagaglia, 2001). In this sense, *N. pygmaea* depicted by these authors can be regarded as a synonym of *N. aff. reynesi* (Fig. 4) and the Umbrian *K. liasiana* are far from their typical forms as they are known in the classical western localities. In the same way, the Swabian *K. liasiana* (Rau, 1905) from the Spinatum Zone are similar to the *K. gibbosula*-type due to their subcircular outline. In this sense, although the morphological differences in the *Koninckella* species are subtle, which leads to some uncertainty, it seems more plausible that the distribution of both *N. pygmaea* and *K. liasiana* was restricted to the westernmost Tethyan basins.

The last episode linking the evolution of koninckinids with the T-OAE is recorded within the Serpentinum Zone in the epicontinental areas, coinciding with the mass extinction boundary. This event is considered as the most conspicuous Mesozoic and Cenozoic extinction for the Phylum

Brachiopoda, as two orders and five superfamilies became extinct in the T-OAE (Vörös, 2002; Comas-Rengifo et al., 2006; García Joral et al., 2011). As is widely recognized, except for the unusual record of koninckinids above the typical isotopic excursions (Reolid et al. 2014b, p. 84), koninckinids became extinct in this event (Vörös, 2002; Comas-Rengifo et al., 2006; García Joral et al., 2011; Comas-Rengifo et al., 2013, 2015). The sudden high sea-bottom warming can be regarded as the most plausible cause of their extinction, as part of a complex scenario contributing to environmental changes (e.g. Karoo-Ferrar igneous eruptions, greenhouse effect, global anoxia, local euxinic conditions).

#### 6.5. Testing the koninckinid cold-seep dependence in the Subbetic koninckinid beds

Recent hypotheses link koninckinid occurrences to the possible existence of hydrocarbon-seeps and a chemosynthesis-based way of life due to an apparent correlation between koninckinid blooms and feasible cold-seep events favored by extensional tectonic phases (Vörös, 2002). As the tectono-sedimentary framework of the Subbetic basin could be a priori propitious to lodging such cold-seeps (*sensu* Vörös, 2002; cf. Campbell et al., 2002; cf. Peckmann and Thiel, 2004; Sandy et al., 2012; Peckmann et al., 2013) and given that one of the main destabilization events of marine gas hydrates took place during the Pliensbachian–Toarcian transition (e.g. Hesselbo et al., 2000, 2007; Beerling et al., 2002; Vörös, 2002; Cohen et al., 2007; Suan et al., 2010), a tentative analysis of the Subbetic koninckinid-bearing deposits has been carried out, focused on various criteria that can play a role as cold-seep proxies. The disposition of the outcrops, where a continuous bed by bed analysis is nearly unworkable, make it unfeasible to perform some customary analyses such as isotopic data or biomarkers, but additional signals can help to test methane-dependence in this area:

*6.5.1. Tectono-sedimentary framework.*- The continuous Early Jurassic rifting stage that led to the drowning of the Subbetic platform by the activity of listric faults in turn generated extensional fractures and crevices in the epiocenic escarpments, and could be a propitious framework to facilitate the cold-seep events (e.g. Vörös, 2002; Sandy et al., 2012; Peckmann et al., 2013) and the

typical environments inhabited by koninckinids (Vörös, 2002). In this sense, Gaillard et al. (2011) also found cold-seep communities linked to active syn-sedimentary faults, and the Lower Cretaceous Carpathian *Peregrinella* deposits, which were established as methane-seep environments (Sandy et al., 2012), show similar depositional scenarios to the Subbetic one. Seep deposits and faunas related to epioceanic seamounts are also confirmed by Gischler et al. (2003) or Little et al. (2004).

6.5.2. *Palaeontological proxies.*- Gregarious behaviour can be included among the key features of the faunal assemblages linked to both recent and ancient cold seeps. They commonly form cluster accumulations as an adaptive response to these very restricted confined habitats. Cold-seep deposits are often characterized by mass occurrences and dense populations of packed individuals (Callender and Powell, 1999; Peckmann et al., 2001, 2007, 2011, 2013; Kiel and Peckmann, 2008; Sandy et al., 2012). In addition to the exceptional profusion of specimens, these habitats show monospecific or oligotypical communities (Callender and Powell, 1999; Gischler et al., 2003; Kaim et al., 2010; Peckmann et al., 2013). Individuals are highly numerous in the Subbetic koninckinid fauna and these beds have very restricted outcrops and stratigraphical distribution; nevertheless neither densely packing nor cluster accumulations are perceived. Furthermore, the faunal diversity is far from being considered as oligotypical, as six different koninckinid species are recorded together with three species of *Nannirhynchia* and several other representative taxa of the typical koninckinid beds (Figs. 2–4). What is more, the remaining standard-sized fauna usually recorded in several Tethyan basins in normal environmental conditions was observed too.

It is also remarkable that koninckinids are recorded in diverse facies (crinoidal grainstone and sandy marlstone) where benthic biota communities abound as this is shown in washed samples and microfacies (Fig. 5). The same occurs with the late Pliensbachian koninckinids of the Bakony (Vörös, 2002, 2009) which are also associated to a very diverse brachiopod assemblage. These data point to an unspecialized polyspecific brachiopod community.

6.5.3. *Sedimentological proxies.*- It is commonly suggested that environmental changes that occurred in the Pliensbachian–Toarcian transition involved destabilization of marine gas hydrates. Potentially, methane can seep from carbonate sediments buried with large amounts of organic matter (cf. Hesselbo et al., 2000; Vörös, 2002, Joseph et al., 2013, among others), frequently contained in black shale deposits. In the Subbetic basin there is no clear evidence of true black shale deposits. Even in the westernmost Subbetic areas, where the lower Toarcian deposits are recorded in more subsident and deeper areas with an expanded and continuous sedimentation, the record of organic-rich facies does not reach sufficiently high TOC values to be regarded as true black shales (Rodríguez-Tovar and Reolid, 2013).

Nevertheless, it should be considered that the physiography of the sea bottom in the Subbetic basin was complex during this timespan, with epi-oceanic swells and semi-grabens generated by the activity of listric faults. As a result of this topographic differentiation and of the consequent feasible local water stratification, oxygen-supplied/-depleted habitats could potentially alternate (Tent-Manclús, 2006; cf. Reolid et al., 2013; cf. Rodríguez-Tovar and Reolid, 2013). In this sense, there is no evidence of black shale deposits or anoxic habitats in the koninckinid-bearing levels herein studied, which does not substantiate their relationship with cold-seep facies and faunas.

Tent-Manclús (2006) described several dark greenish marl levels within the Zegrí Formation, in the same outcrops herein studied but in younger deposits. These levels are barren of benthic infaunal assemblages and were interpreted as representative of slightly reductive conditions near the sediment-water interface during deposition and early diagenetic phases. These conditions are consistent with those documented in the westernmost Tethyan sea bottoms, where organic matter did not reach adequate values to be regarded as black shales (García Joral et al., 2011; Reolid et al., 2012; Rodríguez-Tovar and Reolid, 2013). Overlying these dark levels described by Tent-Manclús (2006), Baeza-Carratalá (2013) recorded *Soaresirhynchia bouchardi*, assigned to the lower–middle part of the Serpentinum Zone, widely regarded as an opportunistic taxon that colonized the Western

Tethys after the mass extinction (García Joral and Goy, 2000; Gahr, 2005, García Joral et al., 2011; Baeza-Carratalá et al., 2011; Baeza-Carratalá, 2013).

Summing up, in this Subbetic area, sediments potentially assignable to the black shale deposition event widely recorded in the Western Tethys and related to the T-OAE are stratigraphically younger than the koninckinid-bearing beds, and they are not typified by any brachiopod fauna or black shales. Koninckinid beds recorded in older levels are therefore unlinked to any stratigraphical or sedimentological features that indicate a possible cold-seep event.

*6.5.4. Petrographical proxies.*- Fossil cold-seep deposits recurrently show distinctive petrographical attributes and microfabrics. Characteristics such as clotted micrite, fibrous, banded and bothryoidal cement or framboidal pyrite, even in the form of aggregations or laminae, are typically found in the methane-seep carbonates (Campbell et al., 2002; Peckmann and Thiel, 2004; Peckmann et al., 2007, 2011; Hammer et al., 2011; Kuechler et al., 2012; Sandy et al., 2012; Kiel et al., 2013; Kaim et al., 2013). These features are completely absent in the lithologies herein studied and petrographic evidences (Fig. 5) reveal that Subbetic koninckinid beds could not be interpreted as seep deposits.

*6.5.5. Geochemical proxies.*- Koninckinid blooms coinciding with isotopical  $\delta C^{13}$  excursions in the late Pliensbachian–early Toarcian (Vörös, 2002 and Fig. 8) might link koninckinid faunas to methane based communities. These fluctuations can be correlated with gas hydrate releases (Hesselbo et al., 2000) and also coincide with the well-documented increase of the bottom-water palaeotemperatures previously exposed as a conditioning factor of the koninckinid distribution pattern. In the same way, reductive conditions and/or anoxia usually prevail in the koninckinid occurrences linked to black shales as was discussed in the sedimentological proxies. Nevertheless, elemental geochemical analysis (Table 1, Fig. 6) reveals that no signs of reductive or anoxic conditions can be inferred for the koninckinid-bearing deposits of the easternmost Subbetic. Similarly, in the analogous koninckinid occurrences of the Bakony (Vörös, 2002, 2009) the geochemical analyses did not support the cold-seep hypothesis either.

## 7. Conclusions.

The koninckinid fauna recorded in the late Pliensbachian–early Toarcian from the easternmost Subbetic basin is palaeobiogeographically consistent with the course of the previously well-established clockwise migration route towards the higher latitude Atlantic basins, supporting the strategy of dispersion put forward by Vörös (2002).

Koninckinids are a suitable group to shed light on the biotic crisis suffered by the brachiopod fauna during one of the most conspicuous mass extinction events in the evolutionary history of the Phylum Brachiopoda. The analysis of their latter occurrences and evolution can be used as a precursor signal of a multi-phased interval with episodes of changing environmental conditions whose onset can be detected from the Elisa–Mirabile? subzones lasting up to the early Toarcian extinction boundary in the lowermost Serpentinum Zone.

In the koninckinid migration pattern from the intra-Tethyan basins to the NW-European platforms, several stages that influenced the evolution of the group are proposed:

- a) The onset of the progressive warming episode in the Pliensbachian–Toarcian transition (Elisa–Mirabile? subzones) triggered a koninckinid fauna exodus stage from the eastern and central Tethys areas toward the westernmost Mediterranean margins (e.g. the Subbetic epicontinental platforms), where they found a suitable habitat to colonize. This migratory episode did not involve changes in the oxygen-supply conditions of the seafloor.
- b) In a second stage, koninckinids show an adaptive response to more adverse environmental conditions in the westernmost Tethyan margin (North-African basins). This turnover represented a replacement of species involving a general decrease in size and diversity loss.
- c) An escape and extinction phase is detected in the Atlantic areas from the mid-Polymorphum Zone onwards, when mostly miniaturized and oligotypical koninckinid faunas spread widely over the Atlantic NW-European basins (Portugal, Normandy and South England) withdrawing from the more intra-Tethyan basins.

d) In the extinction boundary (lowermost Serpentinum Zone), koninckinids became extinct together with many other brachiopod groups, probably as a result of high sea-bottom warming helped by a complex environmental scenario.

The koninckinid migration in its last stages is independent not only of palaeogeographic bioprovinciality, but it is also unrelated to a facies-controlled pattern. The anoxic/suboxic environmental conditions should only be considered as a minor factor of partial control since well-oxygenated conditions are noted in the intra-Tethyan basins and this factor is only noticeable in a second westward migratory stage (with dwarf taxa and oligotypical assemblages).

A first overview analyzing the likelihood of Subbetic koninckinids cold seep-dependence suggests a radiation independent of methane releases in the Subbetic basin.

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### **References**

- Aberhan, M., Fürsich, F.T., 1997. Diversity analysis of Lower Jurassic bivalves of the Andean Basin and the Pliensbachian–Toarcian mass extinction. *Lethaia* 29, 181–195.
- Ager, D.V., 1990. British Liassic Terebratulida (Brachiopoda) Part I. Monograph of the Palaeontographical Society, London 582, 143, 1–39.

- Alm ras, 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.
- Alm ras, Y., Faur , P., 1990. Histoire des brachiopodes liasiques dans la Tethys occidentale: les crises et l' cologie. *Cahiers de l'Universit  Catholique de Lyon Sciences* 4, 1–12.
- Alm ras, Y., Elmi, S., Mouterde, R., Ruget, C., Rocha, R., 1988. Evolution Pal og ographique du Toarcien et influence sur les peuplements, In: Rocha, R.B., Soares, A.F. (Eds.), *International Symposium on Jurassic Stratigraphy*, pp. 687–698 (Lisboa).
- Alm ras, Y., Boullier, A., Laurin, B., 1991. Les zones de Brachiopodes du Jurassique en France. *Annales scientifiques de l'Universit  de Franche-Comt  Besan on, G ologie* 4, 3–30.
- Alm ras, Y., Elmi, S., Faur , P., 2007. Les Brachiopodes Liasiques d'Algerie Occidentale. *Documents des Laboratoires de G ologie Lyon* 163, 3–241.
- Aurell, M., Mel ndez, G., Ol rız, F., B denas, B., Caracuel, J., Garc a-Ramos, J.C., Goy, A., Linares, A., Quesada, S., Robles, S., Rodr guez-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.
- Arias, C., 2013. The Early Toarcian (Early Jurassic) ostracod extinction events in the Iberian Range: The effect of temperature changes and prolonged exposure to low dissolved oxygen concentrations. *Palaeogeography, Palaeoclimatology, Palaeoecology* 387, 40–55.
- Az ma, J., 1977.  tude g ologique des zones externes des Cordill res B tiques aux confins des provinces d'Alicante et de Murcie (Espagne). Unpublished Doctoral Thesis, Universit  Pierre et Marie Curie, Paris VI, 393 pp.
- Baeza-Carratal , J.F., 2008. Patrimonio paleontol gico en la colecci n Jim nez de Cisneros y su aplicaci n al estudio de los braqui podos del Jur sico Inferior en la Cordillera B tica Oriental (provincias Alicante y Norte de Murcia). Unpublished PhD Thesis. Universidad Alicante, 906 pp.
- Baeza-Carratal , J.F., 2011. New Early Jurassic brachiopods from the Western Tethys (Eastern Subbetic, Spain) and their systematic and paleobiogeographic affinities. *Geobios* 44, 345–360, sup. 1–9.
- Baeza-Carratal , J.F., 2013. Diversity patterns of Early Jurassic brachiopod assemblages from the westernmost Tethys (Eastern Subbetic). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 381–382, 76–91.
- Baeza-Carratal , J.F., Garc a Joral, F., Tent-Mancl s, J.E., 2011. Biostratigraphy and palaeobiogeographic affinities of the Jurassic brachiopod assemblages from Sierra Espu a (Mal guide Complex, Internal Betic Zones, Spain). *Journal of Iberian Geology* 37 (2), 137–151.
- Baeza-Carratal , J.F., Giannetti, A., Tent-Mancl s, J.E., Garc a Joral, F., 2014. Evaluating taphonomic bias in a storm-disturbed carbonate platform. Effects of compositional and environmental factors in Lower Jurassic brachiopod accumulations (Eastern Subbetic basin, Spain). *Palaios* 29, 55–73.
- Bailey, T.R., Rosenthal, Y., McArthur, J.M., van de Schootbrugge, B., Thirlwall, M.F., 2003. Paleooceanographic changes of the Late Pliensbachian–Early Toarcian interval: a possible link to the genesis of an Oceanic Anoxic Event. *Earth and Planetary Science Letters* 212, 307–320.



- Bassoulet, J.P., Baudin, F., 1994. Le Toarcien inférieur: une période de crise dans les bassins et sur les plateformes carbonatées de l'Europe du Nord-Ouest et de la Téthys. *Geobios. Mém. Spec.* 17, 645–654.
- Bassoulet, J.P., Elmi, S., Poisson, A., Ricou, L.E., Cecca, F., Belli3n, Y., Giraud, R., Baudin, F., 1993. Middle Toarcian (184–182 Ma.). In: J. Dercourt, L.E. Ricou, B. Vrielynck (Eds.), *Atlas of Tethys Palaeoenvironmental Maps*. Beicip-Franlab, Rueil-Malmaison.
- Beerling, D.J., Lomas, M.R., Gr3ocke, D.R., 2002. On the nature of methane gas-hydrate dissociation during the Toarcian and Aptian Oceanic anoxic events. *American Journal of Science* 302, 28–49.
- Bilotta, M., Venturi, F., Sassaroli, S., 2010. Ammonite faunas, OAE and the Pliensbachian–Toarcian boundary (Early Jurassic) in the Apennines. *Lethaia* 43, 357–380.
- Bittner, A., 1888. 3ber Koninckiniden des alpinen Lias. *Jahrbuch der kaiserlich-k3niglichen geologischen Reichsanstalt* 37, 281–292.
- Bittner, A., 1894. Neue Koninckiniden des alpinen Lias. *Jahrbuch der kaiserlich-k3niglichen geologischen Reichsanstalt* 43, 133–144.
- Bjerrum, C.J., Surlyk, F., Callomon, J.H., Slingerland, R.L., 2001. Numerical paleoceanographic study of the Early Jurassic Transcontinental Laurasian Seaway. *Paleoceanography* 16, 390–404.
- Braga, J.C., 1983. Ammonites del Domerense de la zona Subb3etica (Cordilleras B3eticas, S. de Espa3a). Doctoral Thesis. Universidad Granada, 410 pp.
- Callender, W.R., Powell, E.N., 1999. Why did ancient chemosynthetic seep and vent assemblages occur in shallower water than they do today? *International Journal of Earth Sciences* 88, 377–391.
- Campbell, K.A., Farmer, J.D., Des Marais, D., 2002. Ancient hydrocarbon seeps from the Mesozoic convergent margin of California: carbonate geochemistry, fluids and palaeoenvironments. *Geofluids* 2, 63–94.
- Canavari, M., 1883. Contribuzione III alla conoscenza dei Brachiopodi degli strati a Terebratula Aspasia Mgh. nell'Appennino Centrale. *Atti della Societ3 Toscana di Scienze Naturali* 6, 70–110.
- Caracuel, J.E., Fern3ndez-L3pez, S.R., Tent-Mancl3s, J.E., Y3benes, A., 2004. Itinerario paleontol3gico por el Cerro de La Cruz (Sierra del Reclot). In: Alfaro, P., Andreu, J.M., Est3vez, A., Tent-Mancl3s, J.E., Y3benes, A. (Eds.), *Geolog3a de Alicante*, pp. 245–260.
- Cariou, E., Hantzpergue, P., 1997. Groupe Fran3ais d'3tudes du Jurassique, biostratigraphie du Jurassique ouest-europ3en et m3diterran3en. Zonations parall3les et distribution des invert3br3s et microfossiles. *Bulletin des Centres de Recherches Exploration-Production d'Elf-Aquitaine* 17, 1–400.
- Caruthers A.H., Smith, P.L., Gr3ocke, D.R., 2013. The Pliensbachian–Toarcian (Early Jurassic) extinction, a global multi-phased event. *Palaeogeography, Palaeoclimatology, Palaeoecology* 386, 104–118.
- Cecca, F., Macchioni, F., 2004. The two Early Toarcian (Early Jurassic) extinction events in ammonoids. *Lethaia* 37, 35–56.
- Cohen, A.S., Coe, A.L., Kemp, D.B., 2007. The Late Palaeocene–Early Eocene and Toarcian (Early Jurassic) carbon isotope excursions: a comparison of their time scales, associated environmental changes, causes and consequences. *Journal of the Geological Society* 164, 1092–1108.

- 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 (1), 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*, in press.
- Davidson, T., 1876–1878. A monograph of the British fossil Brachiopoda 4 (2), Triassic-Jurassic Supplement. *Palaeontographical Society, London*, 73–242.
- Dera, G., Neige, P., Dommergues, J.L., Fara, E., Laffont, R., Pellenard, P., 2010. High resolution dynamics of Early Jurassic marine extinctions: the case of Pliensbachian–Toarcian ammonites (Cephalopoda). *Journal of the Geological Society of London* 167, 21–33
- Deslongchamps, E.E., 1853. Mémoire sur les genres *Loeptaena* et *Thecidea* des terrains Jurassiques du Calvados. *Mémoires de la Société Linnéenne de Normandie* 9, 213–250.
- 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.
- Elmi, S., Roulleau, L., Gabilly, J., Mouterde, R., 1997. Toarcien. Biostratigraphie du Jurassique ouest-européen et méditerranéen: zonations parallèles et distribution des invertébrés et microfossiles. In: Cariou, E., Hantzpergue, P. (Eds.). *Bulletin des Centres de Recherches Exploration-Production d'Elf-Aquitaine* 17, 25–36.
- Fraguas, A., Young, J.R., 2011. Evolution of the coccolith genus *Lotharingius* during the Late Pliensbachian–Early Toarcian interval in Asturias (N Spain). Consequences of the Early Toarcian environmental perturbations. *Geobios* 44, 361–375.
- 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.
- Gaillard, C, Néraudeau, D., Thierry, J., 2011. *Tithonia oxfordiana*, a new irregular echinoid associated with Jurassic seep deposits in south-east France. *Palaeontology* 54, 35–752.
- 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.
- Gemmellaro, G.G., 1874. Sopra alcuni faune giuresi e liasiche della Sicilia. *Studi paleontologici* III. Sopra i fossili della zona con *Terebratula Aspasia* Menegh. della provincia di Palermo e di Trapani. *Giornale di Scienze Naturali et Economiche di Palermo* 10, 53–112.

- Gemmellaro, G.G., 1886. Sugli strati con *Leptaena* nel Lias superiore di Sicilia. Bolletino Reale Comitato Geologico Italiano, ser. 2, 7 (5-6): 156–170, (9-10): 341–359.
- Gischler, E., Sandy, M.R., Peckmann, J., 2003. *Ibergirhynchia contraria* (F.A. Roemer, 1850), an early Carboniferous seep-related rhynchonellide brachiopod from the Harz Mountains, Germany - A possible successor to *Dzieduszyckia*? Journal of Paleontology 77, 293–303.
- Gómez, J.J., Goy, A., 2011. Warming-driven mass extinction in the Early Toarcian (Early Jurassic) of northern and central Spain. Correlation with other time-equivalent European sections. Palaeogeography, Palaeoclimatology, Palaeoecology 306, 176–195.
- Gómez, J.J., Goy, A., Canales, M.L., 2008. Seawater temperature and carbon isotope variations in belemnites linked to mass extinction during the Toarcian (Early Jurassic) in Central and Northern Spain. Comparison with other European sections. Palaeogeography, Palaeoclimatology, Palaeoecology 258, 28–58.
- Goy, A., Comas-Rengifo, M.J., Arias, C., García Joral, F., Gómez, J.J., Herrero, C., Martínez, G., Rodrigo, A., 1997. El Tránsito Pliensbachense/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., 1986. The Pliensbachian and Tithonian extinction events. Nature 319, 765–768.
- Hallam, A., 1987. Radiations and extinctions in relation to environmental change in the marine Lower Jurassic of northwest Europe. Paleobiology 13, 152–168.
- Hammer, O., Nakrem, H.A., Little, C.T.S., Hryniewicz, K., Sandy, M.R., Hurum, J.H., Druckenmiller, P., Knutsen, E.M., Høyberget, M., 2011. Hydrocarbon seeps from close to the Jurassic–Cretaceous boundary, Svalbard. Palaeogeography, Palaeoclimatology, Palaeoecology, 306, 15–26.
- Harazim, D., van de Schootbrugge, B., Sorichter, K., Fiebig, J., Weug, A., Suan, G., Oschmann, W., 2013. Spatial variability of watermass conditions within three European Epicontinental Seaways during the Early Jurassic (Pliensbachian–Toarcian). Sedimentology 60, 359–390.
- Harries, J.P., Little, C.T.S., 1999. The Early Toarcian (Early Jurassic) and the Cenomanian–Turonian (Late Cretaceous) mass extinctions: similarities and contrasts. Palaeogeography, Palaeoclimatology, Palaeoecology 154, 39–66.
- Hesselbo, S.P., Gröcke D.R., Jenkyns, H.C., Bjerrum, C.J., Farrimond, P., Morgans-Bell, H.S., Green, O.R., 2000. Massive dissociation of gas hydrate during a Jurassic oceanic anoxic event. Nature 406, 392–395.
- Hesselbo, S.P., Jenkyns, H.C., Duarte, L.V., Oliveira L.C.V., 2007. Carbon-isotope record of the Early Jurassic (Toarcian) oceanic anoxic event from fossil wood and marine carbonate (Lusitanian Basin, Portugal). Earth and Planetary Science Letters 253, 455–470.
- Iñesta, M., 1988. Braquiópodos Liásicos del Cerro de La Cruz (La Romana, Prov. Alicante, España). Mediterránea, Serie Geológica 7, 45–64.
- Jach, R., 2005. Storm-dominated deposition of the Lower Jurassic crinoidal limestones in the Krížna unit, Western Tatra Mountains, Poland. Facies 50, 561–572.
- Jenkyns, H.C., 1985. The early Toarcian and Cenomanian–Turonian anoxic events in Europe: comparisons and contrasts. Geol. Rundsch. 74, 505–518.
- Jenkyns, H.C., 1988. The Early Toarcian (Jurassic) anoxic event: stratigraphy, sedimentary and geochemical evidence. American Journal of Science 288, 101–151.

- Jenkyns, H.C., 2003. Evidence for rapid climate change in the Mesozoic–Palaeogene greenhouse world. *Philosophical Transactions of the Royal Society of London* 361, 1885–1916.
- Jenkyns, H.C., Clayton, C.J., 1986. Black shales and carbon isotopes in pelagic sediments from the Tethyan Lower Jurassic. *Sedimentology* 33, 87–106.
- Jenkyns, H.C., Gale, A.S., Corfield, R.M., 1994. Carbon- and oxygen-isotope stratigraphy of the English Chalk and Italian Scaglia and its palaeoclimatic significance. *Geological Magazine* 131, 1–34.
- Jiménez, A.P., Jiménez de Cisneros, C., Rivas, P., Vera, J.A., 1996. The Early Toarcian Anoxic Event in the Westernmost Tethys (Subbetic): Paleogeographic and Paleobiogeographic significance. *Journal of Geology* 104, 399–416.
- Jiménez, A.P., Rivas, P., 2007. El OAE Toarciense en la secuencia de la Fuente de la Vidriera, Zona Subbética, región de Caravaca (Murcia). In: Aguirre, J., Company, M., Rodríguez-Tovar, F.J. (Eds.), 23 Jornadas de la Sociedad Española de Paleontología, Caravaca, Field Trip Guidebook. University of Granada, pp. 3–16.
- Jiménez de Cisneros, D., 1923. La Fauna de los estratos de “Pygope Aspasia” Menegh. del Liásico Medio del Rincón de Egea en el W de la provincia de Murcia: Trabajos del Museo Nacional de Ciencias Naturales, Serie Geológica 30, 1–55.
- Jiménez de Cisneros, D., 1927. Nota sobre braquiópodos liásicos. Asociación española para el Progreso de las Ciencias. Sección IV, Ciencias Naturales, 203–207.
- Joseph, C., Campbell, K.A., Torres, M.E., Martin, R.A., Pohlman, J.W., Riedel, M., Rose, K., 2013. Methane-derived authigenic carbonates from modern and paleoseeps on the Cascadia margin: Mechanisms of formation and diagenetic signals. *Palaeogeography, Palaeoclimatology, Palaeoecology* 390, 52–67.
- Kaim, A., Bitner, M.A., Jenkins, R.G., Hikida, Y.A., 2010. Monospecific assemblage of terebratulide brachiopods in the Upper Cretaceous seep deposits of Omagari, Hokkaido, Japan. *Acta Palaeontologica Polonica* 55, 73–84.
- Kaim, A., Skupien, P., Jenkins, R.G., 2013. A new Lower Cretaceous hydrocarbon seep locality from the Czech Carpathians and its fauna. *Palaeogeography, Palaeoclimatology, Palaeoecology* 390, 42–51.
- Kemp, D.B., Coe, A.L., Cohen, A.S., Schwark, L., 2005. Astronomical pacing of methane release in the Early Jurassic period. *Nature* 437, 396–399.
- Kiel, S., Peckmann, J., 2008. Paleoecology and evolutionary significance of an early Cretaceous *Peregrinella*-dominated hydrocarbon-seep deposit on the Crimean peninsula. *Palaios* 23, 751–759.
- Kiel, S., Birgel, D., Campbell, K.A., Crampton, J.S., Schiøler, P., Peckmann, J., 2013. Cretaceous methane-seep deposits from New Zealand and their fauna. *Palaeogeography, Palaeoclimatology, Palaeoecology* 390, 17–34.
- Kolbe, S.E., Zambito IV, J.J., Brett, C.E., Wise, J.L., Wilson, R.D., 2011. Brachiopod shell discoloration as an indicator of taphonomic alteration in the deep-time fossil record. *Palaios* 26, 682–692.
- Kuechler, R.R., Birgel, D., Kiel, S., Freiwald, A., Goedert, J.L., Thiel, V., Peckmann, J., 2012. Miocene methane-derived carbonates from southwestern Washington, USA and a model for silicification at seeps. *Lethaia* 45, 259–273.

- Little, C.T.S., Benton, M.J., 1995. Early Jurassic mass extinction: A global long-term event. *Geology* 23, 495–498.
- Little, C.T.S., Danelian, T., Herrington, R.J., Haymon, R.M., 2004. Early Jurassic hydrothermal vent community from the Franciscan Complex, California. *Journal of Paleontology* 78, 542–559.
- Macchioni, F., Cecca, F., 2002. Biodiversity and biogeography of middle–late liassic ammonoids: implications for the Early Toarcian mass extinction. *Geobios Mémoire spécial* 24, 165–175.
- Mailliot, S., Mattioli, E., Guex, J., Pittet, B., 2006. The early Toarcian anoxia, a synchronous event in the Western Tethys? An approach by quantitative biochronology (Unitary Associations), applied on calcareous nanofossils. *Palaeogeography, Palaeoclimatology, Palaeoecology* 240, 562–586.
- Manceñido, M.O., 1978. Studies of Early Jurassic brachiopoda and their distribution, with special reference to Argentina. Unpublished Doctoral Thesis, University College of Swansea, University of Wales, 481 p.
- Manceñido, M.O., 1993. Early Jurassic Brachiopods from Greece: a review. In: Pálffy, J., Vörös, A. (Eds.): *Mesozoic Brachiopods of Alpine Europe*. Hungarian Geological Society, Budapest, 79–100.
- Mattioli, E., Erba, E., 1999. Biostratigraphic synthesis of calcareous nanofossil events in the Tethyan Jurassic. *Rivista Italiana Paleontologia Stratigrafia* 105, 343–376.
- Mattioli, E., Plancq, J., Boussaha, M., Duarte L.V., Pittet B., 2013. Calcareous nanofossil biostratigraphy: new data from the Lower Jurassic of the Lusitanian Basin. *Comunicações Geológicas* 100 Especial I, 69–76.
- Methodiev, L.S., Savov, I.P., Gröcke, D.R., Wignall, P.B., Newton, R.J., Andreeva P.V., Koleva-Rekalova, E.K., 2014. Paleoenvironmental conditions recorded by  $^{87}\text{Sr}/^{86}\text{Sr}$ ,  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  in late Pliensbachian–Toarcian (Jurassic) belemnites from Bulgaria. *Palaeogeography, Palaeoclimatology, Palaeoecology* 409, 98–113.
- Molina, J.M., 1987. Análisis de facies del Mesozoico en el Subbético Externo (provincias de Córdoba y Sur de Jaén). Doctoral Thesis, Universidad de Granada, 518 p.
- Pálffy, J., Smith, P.L., 2000. Synchrony between Early Jurassic extinction, oceanic anoxic event, and the Karoo–Ferrar flood basalt volcanism. *Geology* 28, 747–750.
- Peckmann, J., Thiel, V., 2004. Carbon cycling at ancient methane seeps. *Chemical Geology* 205, 443–467.
- Peckmann, J., Gischler, E., Oschmann, W., Reitner, J., 2001. An Early Carboniferous seep community and hydrocarbon-derived carbonates from the Harz Mountains, Germany. *Geology* 29, 271–274.
- Peckmann, J., Campbell, K.A., Walliser, O.H., Reitner, J., 2007. Late Devonian hydrocarbon-seep deposit dominated by Dimerelloid brachiopods, Morocco. *Palaios* 22, 114–122.
- Peckmann, J., Kiel, S., Sandy, M.R., Taylor, D.G., Goedert, J.L., 2011. Mass occurrences of the brachiopod *Halorella* in Late Triassic methane-seep deposits, eastern Oregon. *Journal of Geology* 119, 207–220.
- Peckmann, J., Sandy, M.R., Taylor, D.G., Gier, S., Bach, W., 2013. An Early Jurassic brachiopod-dominated seep deposit enclosed by serpentinite, eastern Oregon, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 390, 4–16
- Perilli, N., Fraguas, A., Comas-Rengifo, M.J., 2010. Reproducibility and reliability of the Pliensbachian calcareous nanofossil biohorizons from the Basque-Cantabrian Basin (Northern Spain): *Geobios* 43, 77–85.

- Pozza, G.C., Bagaglia, A., 2001. A *Koninckella* fauna recorded from the s.s. type-locality of the Marne di M. Serrone Formation (Umbria, Central Italy, Northern Apennine). 1 Part. *Revue de Paléobiologie* 20, 19–29.
- Principi, P., 1910. Brachiopodi del Lias medio di Castel del Monte (presso Acquasparta). *Rivista Italiana di Paleontologia* 16, 63–88.
- Rau, K., 1905. Die Brachiopoden des mittleren Lias Schwabens mit Ausschluss der Spiriferinen. *Geologische und Paläontologische Abhandlungen* 10, 263–355.
- Reggianni, L., Mattioli, E., Pittet, B., Duarte, L.V., Veiga de Oliveira L.C., Comas-Rengifo M.J., 2010. Pliensbachian (Early Jurassic) calcareous nannofossils from the Peniche section (Lusitanian Basin, Portugal): A clue for palaeoenvironmental reconstructions. *Marine Micropaleontology* 75, 1–16
- Renz, C., 1932. Brachiopoden des südschweizerischen und westgriechischen Lias. *Abhandlungen der Schweizerischen Palaeontologischen Gesellschaft* 52, 1–62.
- Reolid, M., Rodríguez-Tovar, F.J., Marok, A., Sebane, A., 2012. The Toarcian Oceanic Anoxic Event in the Western Saharan Atlas, Algeria (North African Palaeomargin): role of anoxia and productivity. *Geological Society of America Bulletin* 124, 1646–1664
- Reolid, M., Nieto, L.M., Sánchez-Almazo, I.M., 2013. Caracterización geoquímica de facies pobremente oxigenadas en el Toarciense Inferior (Jurásico Inferior) del Subbético Externo. *Revista de la Sociedad Geológica de España* 26, 69–84.
- Reolid, M., Marok, A., Sebane, A., 2014a. Foraminiferal assemblages and geochemistry for interpreting the incidence of Early Toarcian environmental changes in North Gondwana palaeomargin (Traras Mountains, Algeria). *Journal of African Earth Sciences* 95, 105–122.
- Reolid, M., Mattioli, E., Nieto, L.M., Rodríguez-Tovar, F.J., 2014b. The Early Toarcian Oceanic Anoxic Event in the External Subbetic (Southiberian Palaeomargin, Westernmost Tethys): geochemistry, nannofossils and ichnology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 411, 79–94.
- Rodríguez-Tovar, F.J., Reolid, M., 2013. Environmental conditions during the Toarcian Oceanic Anoxic Event (T-OAE) in the westernmost Tethys: influence of the regional context on a global phenomenon. *Bulletin of Geosciences* 88, 697–712.
- Rosales, I., Quesada, S., Robles, S., 2004. Paleotemperature variations of Early Jurassic seawater recorded in geochemical trends of belemnites from the Basque–Cantabrian basin, northern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 203, 253–275.
- Ruban, D.A., 2004. Diversity dynamics of Early–Middle Jurassic brachiopods of Caucasus and the Pliensbachian–Toarcian mass extinction. *Acta Palaeontologica Polonica* 49, 275–282.
- Ruban, D.A., 2009. Brachiopod decline preceded the Early Toarcian mass extinction in the Northern Caucasus (northern Neo-Tethys Ocean): a palaeogeographical context. *Revue de Paléobiologie* 28, 85–92.
- Sandoval, J., Bill, M., Aguado, R., O’Dogherty, L., Rivas, P., Morard, A., Guex, J., 2012. The Toarcian in the Subbetic basin (southern Spain): Bioevents (ammonite and calcareous nannofossils) and carbon-isotope stratigraphy. *Palaeogeography, Palaeoclimatology, Palaeoecology* 342–343, 40–63.

- Sandy, M.R., Lazăr, I., Peckmann, J., Birgel, D., Stoica, M., Roban, R.D., 2012. Methane-seep brachiopod fauna within turbidites of the Sinaia Formation, Eastern Carpathian Mountains, Romania. *Palaeogeography, Palaeoclimatology, Palaeoecology* 323–325, 42–59.
- Steinmann, G., 1886. Das Leptaena-Bett bei Gotha. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* 2, 81–85.
- Suan, G., Mattioli, E., Pittet, B., Lécuyer, C., Suchéras-Marx, B., Duarte, L.V., Philippe, M., Reggiani, L., Martineau, F., 2010. Secular environmental precursors to Early Toarcian (Jurassic) extreme climate changes. *Earth and Planetary Science Letters* 290, 448–458.
- Sulser, H., 1999. Die fossilen Brachiopoden der Schweiz und der angrenzenden Gebiete. *Juragebirge und Alpen*. Paläontologischen Institut und Museum der Universität Zürich, 315 pp.
- Tent-Manclús, J.E., 2006. Estructura y estratigrafía de las sierras de Crevillente, Abanilla y Algayat: su relación con la Falla de Crevillente: Doctoral Thesis, Universidad de Alicante, 970 pp., <http://hdl.handle.net/10045/10414>
- Van Veen, G.W., 1969. Geological investigations in the region West of Caravaca. Unpublished Doctoral Thesis, University of Amsterdam, 143 pp.
- 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, 345–464.
- Vörös, A., 1986. Brachiopod palaeocology on a Tethyan Jurassic seamount (Pliensbachian, Bakony Mountains, Hungary). *Palaeogeography, Palaeoclimatology, Palaeoecology* 57, 241–271.
- Vörös, A., 1993. Jurassic Brachiopods of the Bakony Mts. (Hungary): Global and local effects on changing diversity. In: Pálffy, J. Vörös, A. (Eds.). *Mesozoic Brachiopods of Alpine Europe*, Hungarian Geological Society, Budapest, 179–187.
- Vörös, A., 1994. Umbrian Liassic brachiopods in Hungary: review and comparison. *Paleopelagos Special Publications* 1, 357–366.
- Vörös, A., 2002. Victims of the Early Toarcian anoxic event: the radiation and extinction of Jurassic Koninckinidae (Brachiopoda). *Lethaia* 35, 345–357.
- Vörös, A., 2003. Early Jurassic Koninckinids (Athyriridida, Brachiopoda) from Tivoli near Rome, Italy. *Geologica Romana* 36, 169–197.
- 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.
- Wignall, P.B., Bond, D.P.G., 2008. The end-Triassic and Early Jurassic mass extinction records in the British Isles. *Proceedings of the Geologists' Association* 119, 73–84.
- Wignall, P.B., Newton, R.J., Little, C.T.S., 2005. The timing of paleoenvironmental change and cause-and-effect relationships during the Early Jurassic mass extinction in Europe. *American Journal of Science* 305, 1014–1032.

Zakharov, V.A., Shurygin, B.N., Il'ina, V.I., Nikitenko, B.L., 2006. Pliensbachian–Toarcian biotic turnover in North Siberia and the Arctic Region. *Stratigraphy and Geological Correlation* 14, 399–417.

**Figure captions:**

**Fig. 1.** Geological sketch showing (A) the situation of the outcrops within the context of the Betic Cordillera in the Alicante Province, and (B) in the geological map of the broad region studied. 1. Sierra de Orts section; 2. Cerro de la Cruz section; 3. Tarabillo section; 4. El Cantón section; 5. La Alameda section.

**Fig. 2.** Lower Jurassic lithostratigraphical sections from the easternmost Subbetic including koninckinid-bearing levels, also showing the distribution of the remaining brachiopod taxa associated. A. Cerro de la Cruz section. B. Sierra de Orts section. C. Tarabillo section.

**Fig. 3.** Some representative species of koninckinids from the easternmost Subbetic area. Images of each specimen are ordered consecutively in dorsal, ventral, lateral, and anterior views. **1, 2.** *Koninckella gibbosula* (Gemmellaro) from the Cerro de La Cruz section: 1. Specimen CCB.2.Kgi.1; 2. specimen CCB.2.Kgi.2. **3–6.** *Koninckella bolivari* (Jiménez de Cisneros): 3. specimen CCB.3.Kti.1; 4. specimen CCB.3.Kti.2; 5. CCB.3.Kti.3 specimen, from the Cerro de La Cruz section; 6. specimen O.V.TS.6.1, from JdC collection. **7–10.** *Koninckodonta fornicata* (Canavari): all specimens from the Cerro de La Cruz section except for 8 (JdC collection). 7. Specimen CCB.2.Kfo.II.1; 8. Specimen O.X.18.T2.1; 9. Specimen CCB.2.Kfo.I.1; 10. Specimen CCB.2.Kfo.I.2. **11.** *Koninckodonta cf. fornicata* (Canavari): specimen CCB.2.Kst.1 from the Cerro de La Cruz section. **12–14.** *Koninckodonta waehneri* (Bittner) from the Cerro de La Cruz section: 12. Specimen CCB.2.Kwa.1; 13. Specimen CCB.2.Kwa.2; 14. Specimen CCB.2.Kwa.3. **15, 16.** *Koninckodonta davidsoni* (Deslongchamps) from JdC collection: 15. Specimen O.X.17.1; 16. Specimen O.II.17.T3.8.



**Fig. 4.** Some representative taxa associated to the koninckinid fauna from the easternmost Subbetic area (a: dorsal, b: anterior, and c: lateral views). All specimens were coated with magnesium oxide. **1–3.** *Nannirhynchia pilulla* (Schlosser in Böse and Schlosser) from JdC collection. 1. Specimen O.VIII.23.5; 2. Specimen O.IV.1.T2.3; 3. Specimen O.IV.1.T2.4. **4.** *Nannirhynchia* aff. *gemmellaro*i (Parona), specimen O.IV.9.T4.1. **5, 6.** *Nannirhynchia* aff. *reynesi* (Gemmellaro). 5. Specimen O.VIII.23.T1.2; 6. Specimen O.VIII.23.T1.1. **7.** *Orthotoma* sp., specimen CCB.Or.1 severely damaged, from the Cerro de La Cruz section.

**Fig. 5.** Microfacies photographs and SEM EDX-mapping aimed at the analysis of the oxide composition. **A–C.** Crinoidal packstone microfacies. **A.** Polished slab; **B.** Microfacies photograph, **C.** Detail of spiriferinid-section (ventral valve in the upper part). **D–F.** Marly limestone microfacies. Note the presence of oxides and diagenetic halos. **D.** Polished slab; **E.** Microfacies photograph; **F.** Detail of the calcitic cements: note the complete absence of banded cement. **G.** SEM EDX-mapping providing the element distribution in and around the oxides revealing the exclusive presence of iron, calcium and aluminum. **H.** SEM image showing the structure of the oxides and the complete absence of framboids of pyrite. **I.** SEM microphotograph of the ventral valve of the spiriferinid specimen showed in **C**, noting details of the shell microstructure and calcite layers.

**Fig. 6. A.** Mineralogical composition of different koninckinid-bearing levels performed on both crinoidal grainstone (Ta.Z2.Pi) and calcareous sandy marlstone (CC.2.2.pi) powdered samples by X-RD. **B–C.** Geochemical microanalysis performed under SEM with energy dispersive X-ray spectrometry (EDS) on (B) calcareous sandy marlstone (CC.2.2.pi) and (C) crinoidal grainstone (Ta.Z2.Pi) samples.

**Fig. 7.** Palaeogeographical map of the late Pliensbachian–earliest Toarcian (slightly modified after Bassoullet et al., 1993), showing representative westernmost Tethyan localities with koninckinid

fauna records (sources cited in the text) and the main evolution phases suggested. Records from Mediterranean well-oxygenated habitats and those from the epicontinental NW-European areas have been distinguished. Tentative connections or unreliable data are marked with a (?).

**Fig. 8.** Correlation sketch showing the relationship between koninckinid fauna events inferred, isotopic  $\delta C^{13}$  fluctuations and relative palaeotemperature variations around the Subbetic and Northern-Central Iberian marginal platforms. Outline enveloping curves enclosing the main  $\delta C^{13}$  values and deviations and palaeotemperature data are based on García Joral et al. (2011) and Sandoval et al. (2012) and have been redrawn (slightly modified) after Sandoval et al. (2012). All data are plotted against the zonal/ subzonal ammonite zonation.

**Table 1.** Elemental geochemical analyses of selected koninckinid-bearing levels (bulk rock).

CC.2.2.pi: sample of red crinoidal grainstone from Cerro de La Cruz section; Ta.Z2.pi: sample of calcareous sandy marlstone from Tarabillo section. LOI: Loss on ignition.

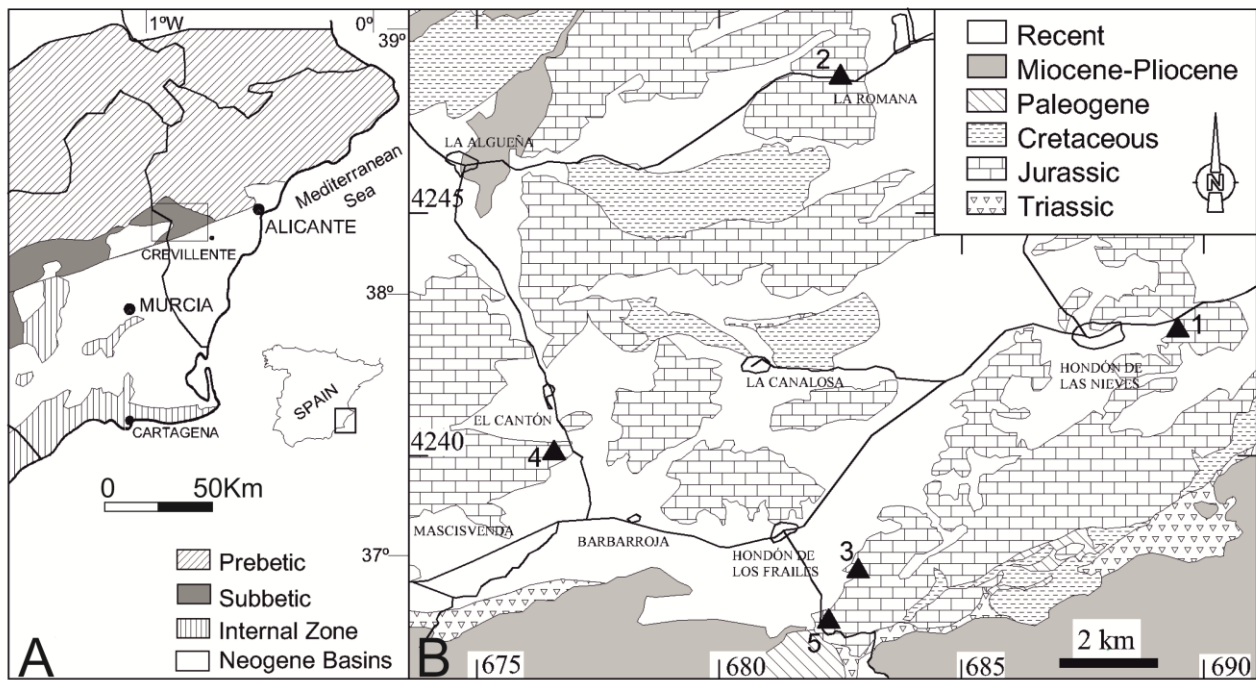


Figure 1

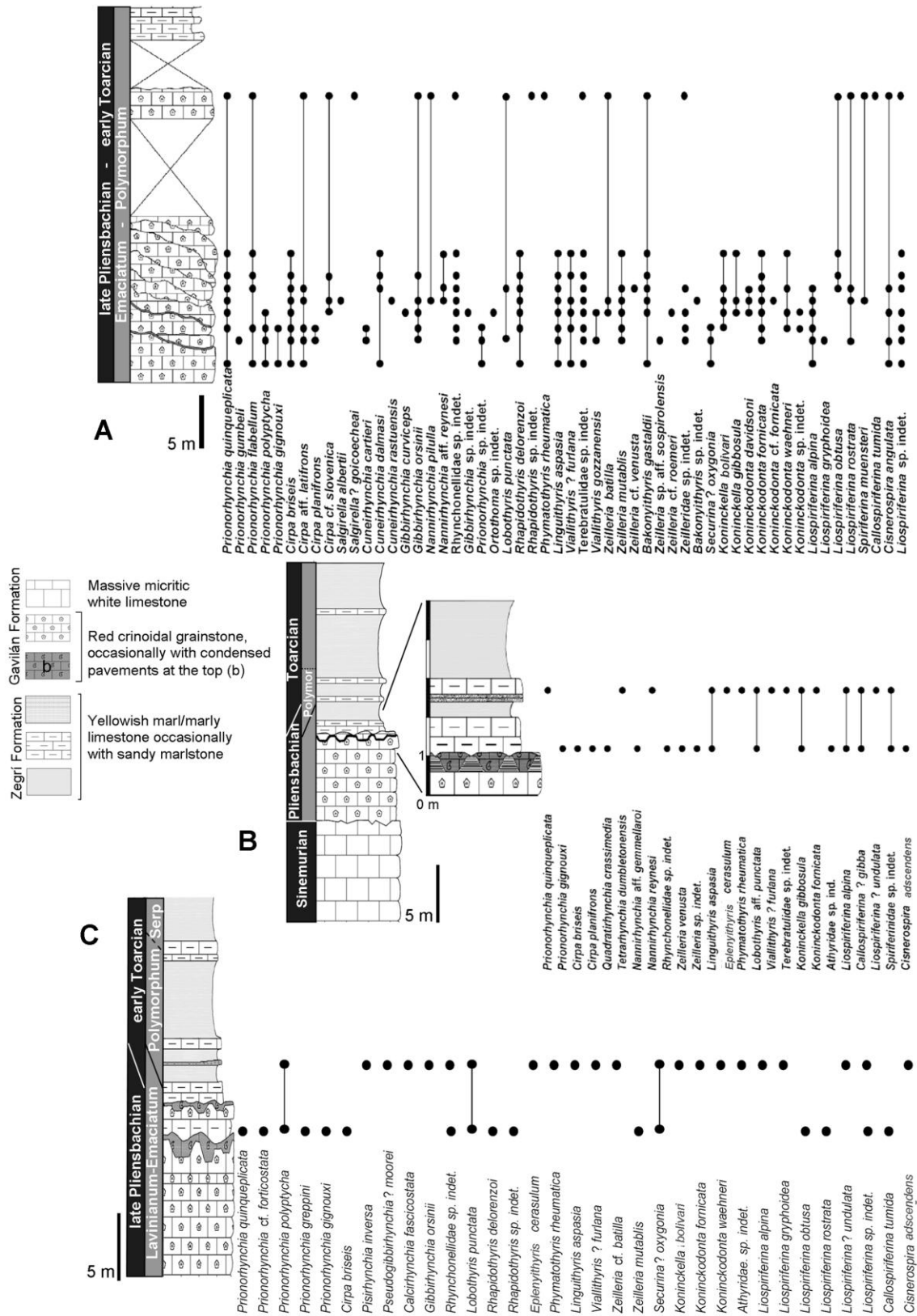


Figure 2

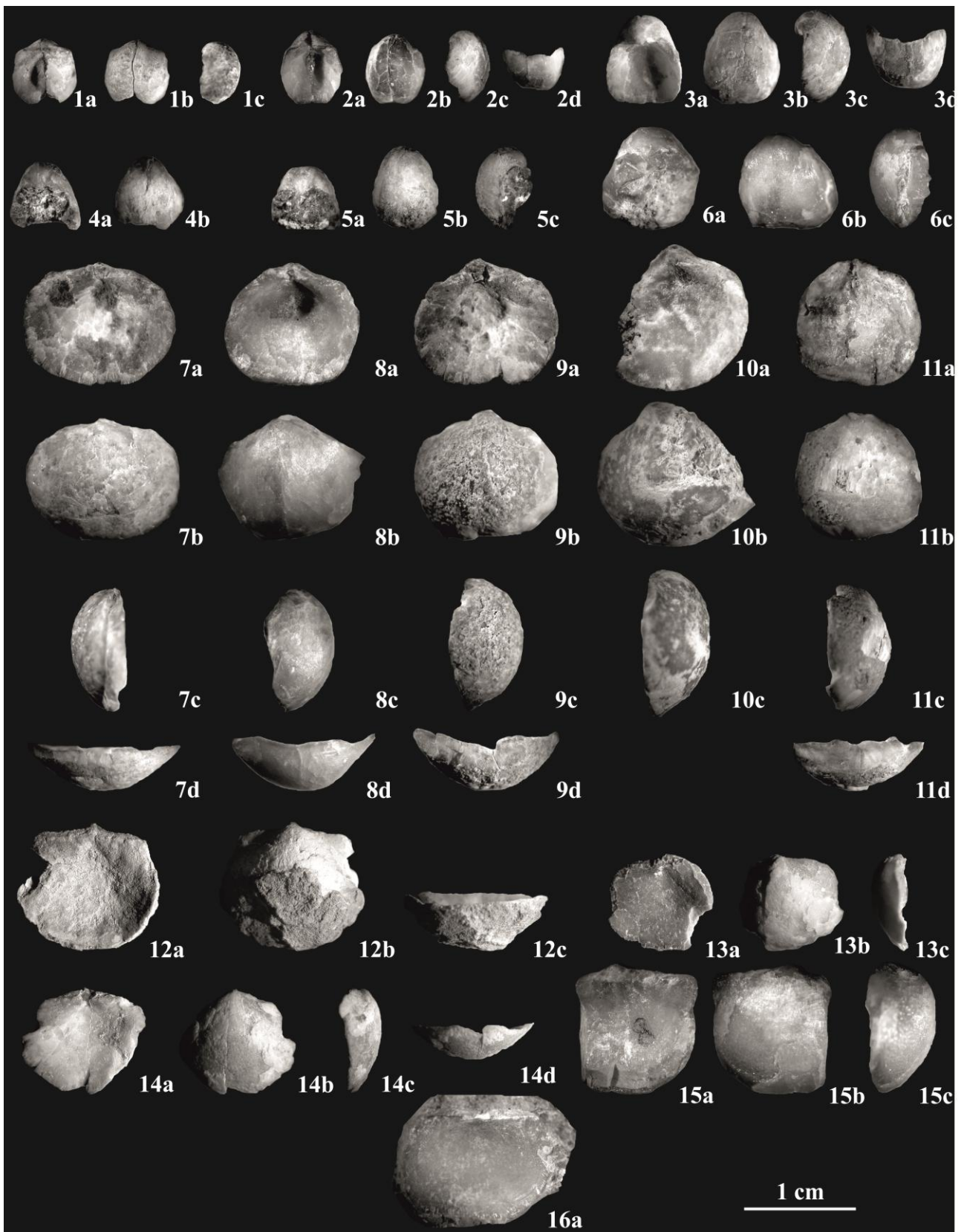


Figure 3

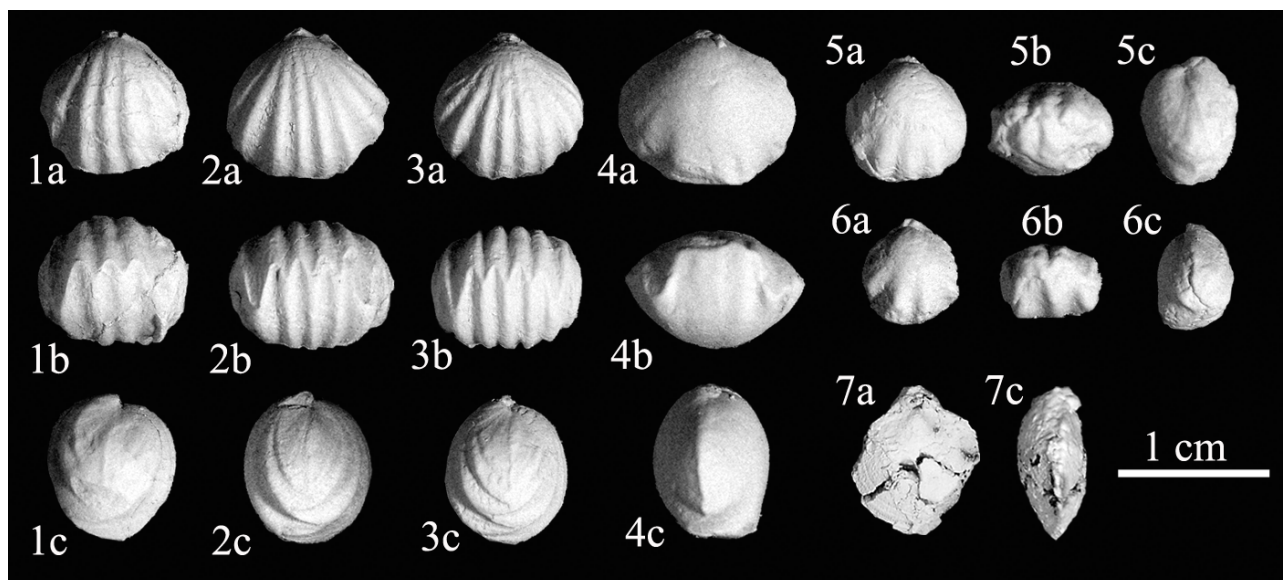


Figure 4

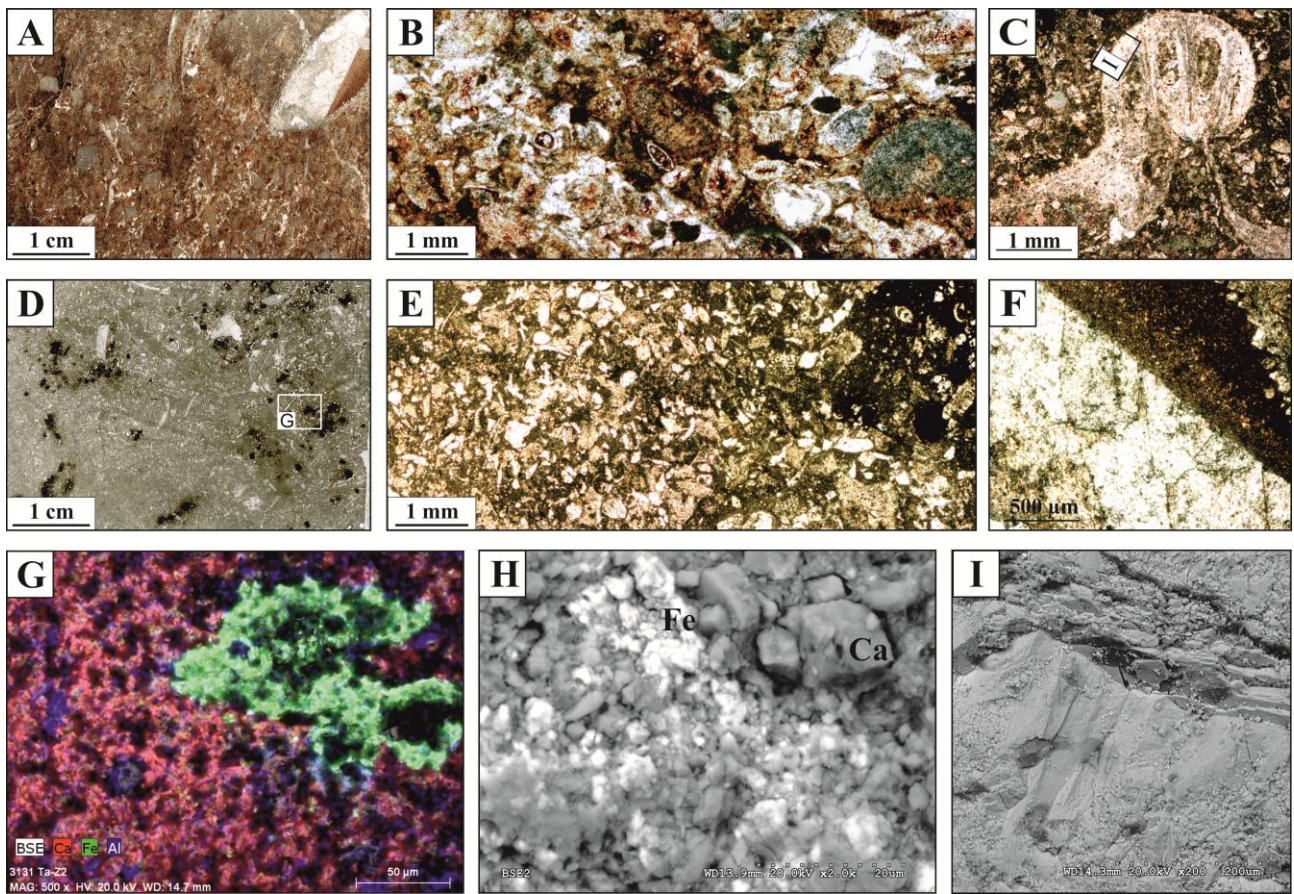


Figure 5

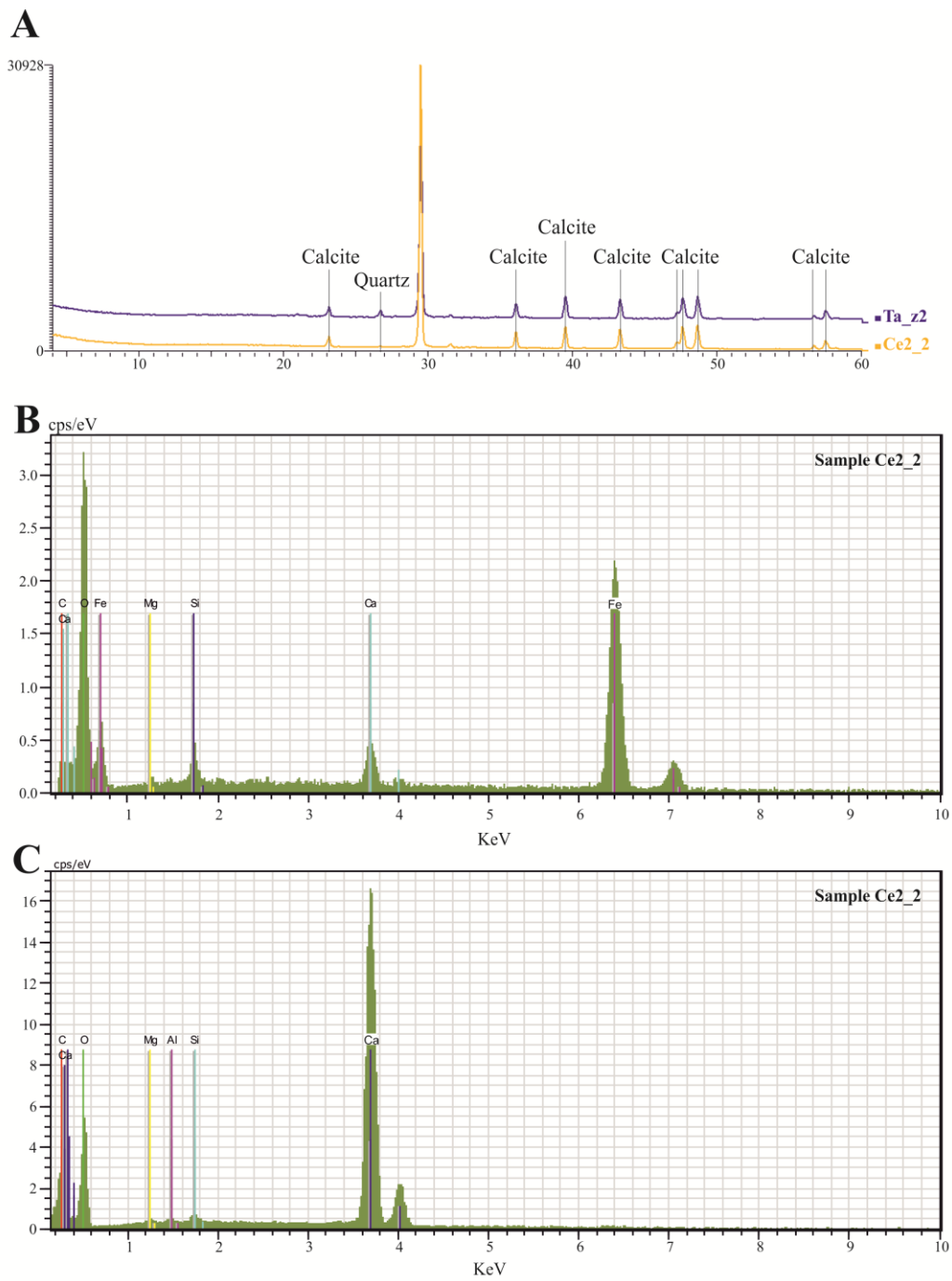


Figure 6



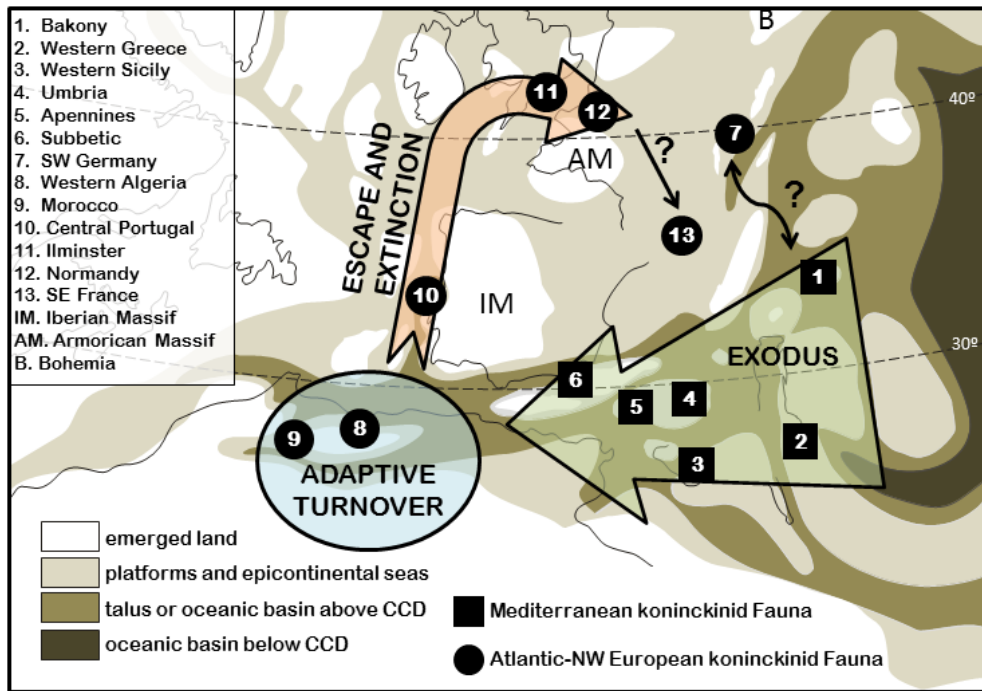


Figure 7

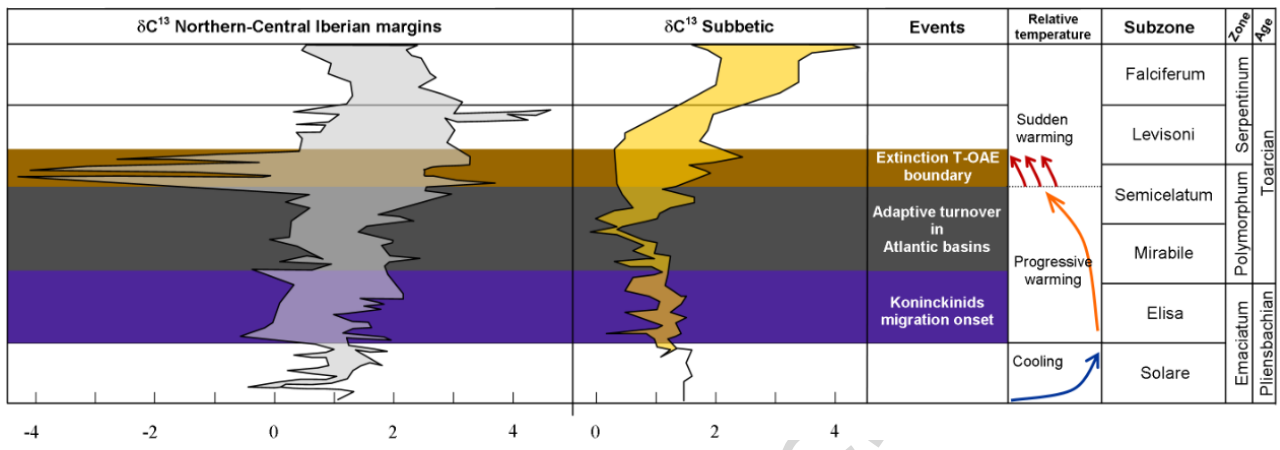
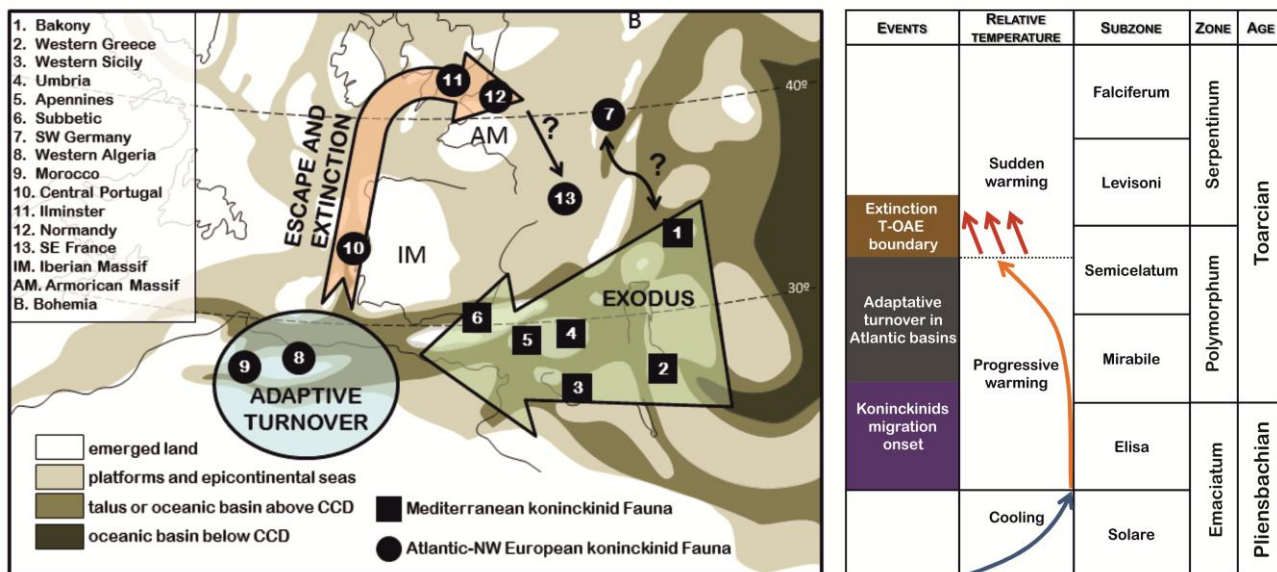


Figure 8

**Table 1**

Elements (%)			Oxides (%)		
	CC-2-2-pi	Ta-Z2-pi		CC-2-2-pi	Ta-Z2-pi
Ca	40,2	33,1	MgO	0,534	0,627
O	18,7	23,5	Al <sub>2</sub> O <sub>3</sub>	0,951	1,912
Si	1,38	6,67	SiO <sub>2</sub>	2,947	14,262
Fe	0,583	2,82	P <sub>2</sub> O <sub>5</sub>	0,122	0,205
Al	0,503	1,01	SO <sub>3</sub>	0,063	0,089
Cl	0,38	0,5	K <sub>2</sub> O	0,179	0,54
Ba	0,349	-	CaO	56,182	46,317
Mg	0,322	0,378	Fe <sub>2</sub> O <sub>3</sub>	0,834	4,028
K	0,149	0,448	BaO	0,39	-
P	0,0532	0,0896	SrO		0,022
S	0,0253	0,0357	TiO <sub>2</sub>		0,141
Sr	<<	0,0189	Cl	0,38	0,5
Cu	-	<<	<b>LOI</b>	37,42	31,36
Ti	-	0,0843			



Graphical Abstract

**Highlights:**

- Koninckinid fauna is a suitable group to illuminate the biotic crisis of Brachiopoda.
- Their final evolution is a precursor signal of the Early Toarcian mass extinction.
- An E-W exodus stage is followed by adaptive response and final extinction phases.
- The migration is independent of provinciality, facies and partly of oxygen supply.
- The radiation in the Subbetic basin seems to be independent of methane releases.