

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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ARTICLE INFO

Article history:

Received 21 October 2014

Received in revised form 26 March 2015

Accepted 6 April 2015

Available online 17 April 2015

Keywords:

Early Jurassic
Mass extinction
Koninckinids
Western Tethys

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 of the paleogeographic 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 noticeable only 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.

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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; Macchioni and Cecca, 2002; Vörös, 2002; Wignall et al., 2005; Wignall and Bond, 2008; Arias, 2013; Caruthers et al., 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 paleobiogeographic pattern (Baeza-Carratalá et al., 2011; Baeza-Carratalá, 2013).

The orders Spiriferinida and Athyridida became extinct as an 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 that of the Paleozoic 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 classic *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).

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Nowadays, copious specimens of koninckinids and of the usually associated fauna have been recorded and taxonomically analyzed 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 Jorál 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 classic *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 paleogeographical 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-seep 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 neighboring Western Tethyan

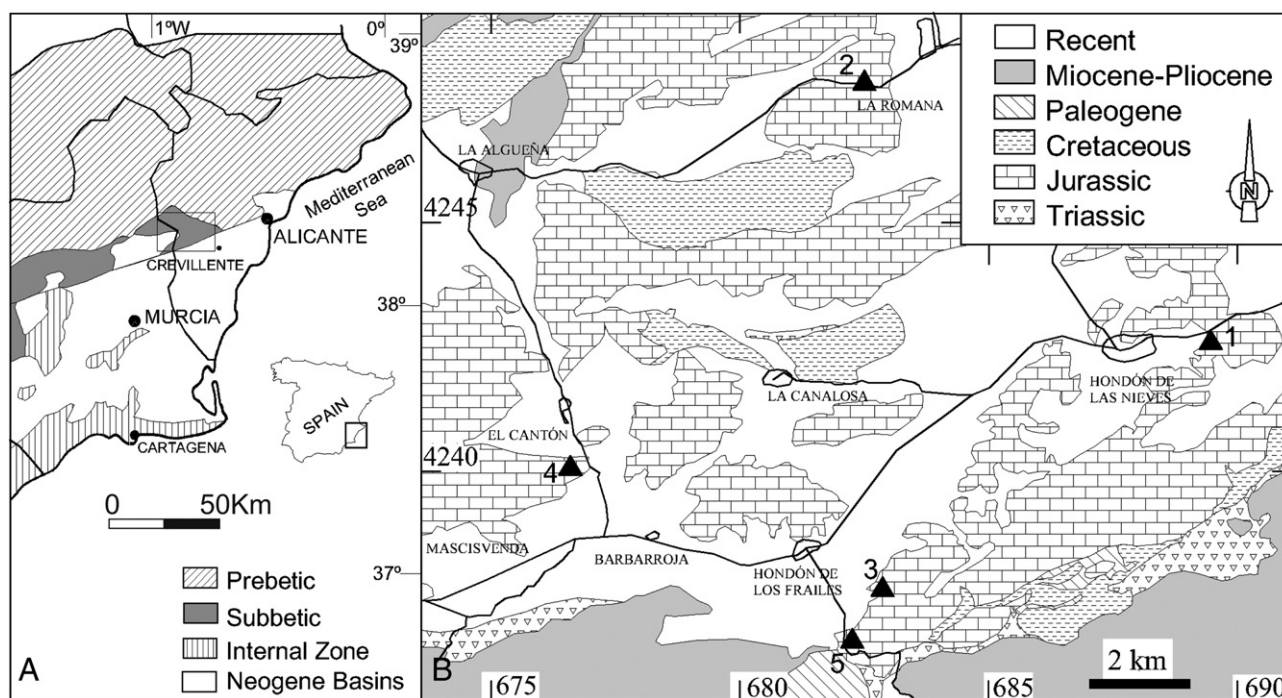


Fig. 1. Geological sketch showing (A) the situation of the outcrops within the context of the Betic Cordillera in the Alicante Province, and (B) in the geological map of the broad region studied. 1. Sierra de Orts section; 2. Cerro de la Cruz section; 3. Tarabillo section; 4. El Cantón section; 5. La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

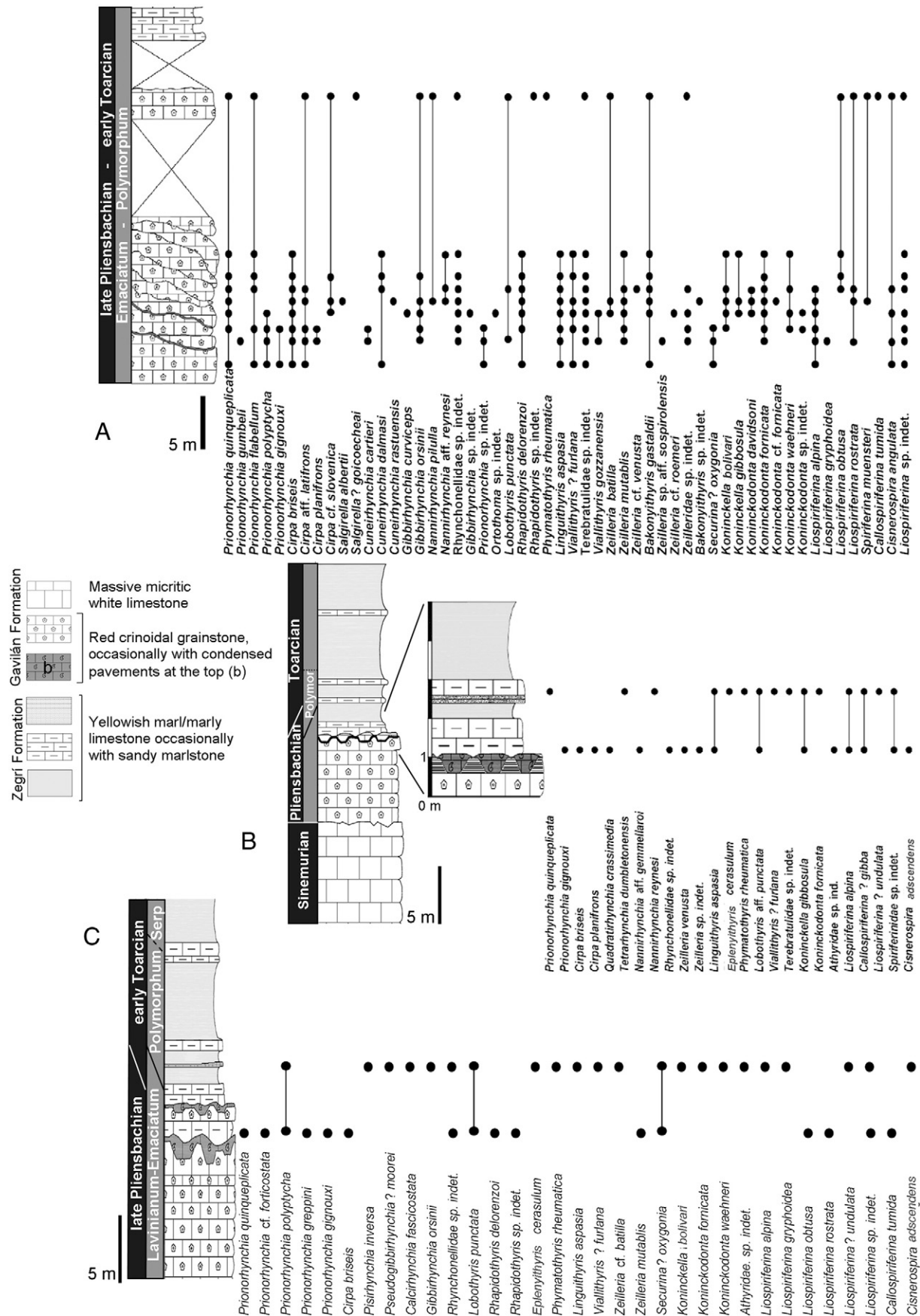


Fig. 2. Lower Jurassic lithostratigraphical sections from the easternmost Subbetic including koninckinid-bearing levels, also showing the distribution of the remaining brachiopod taxa associated. A. Cerro de la Cruz section. B. Sierra de Orts section. C. Tarabillo section.

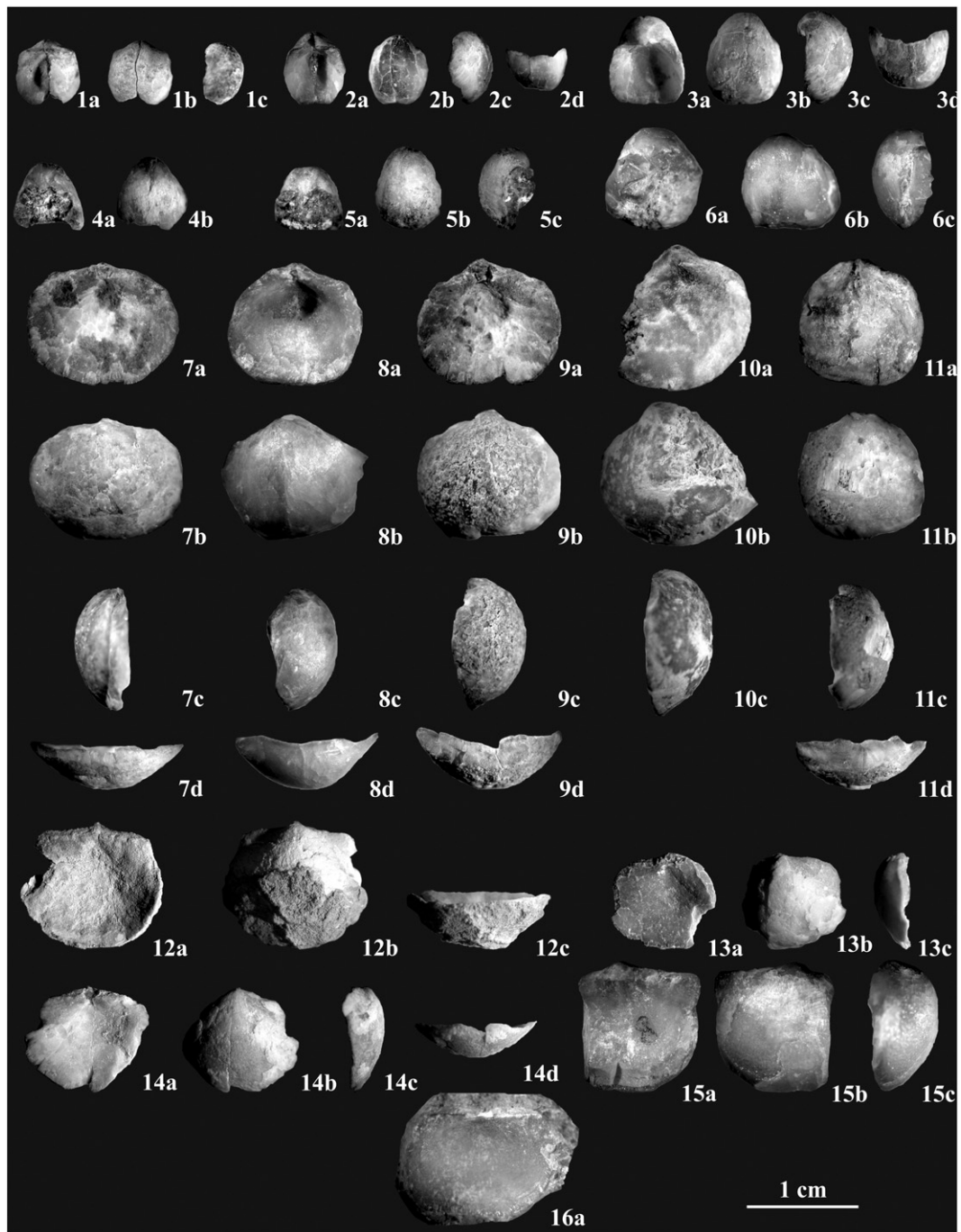


Fig. 3. Some representative species of koninckinids from the easternmost Subbetic area. Images of each specimen are ordered consecutively in dorsal, ventral, lateral, and anterior views. 1, 2. *Koninckella gibbosula* (Gemmellaro) from the Cerro de La Cruz section: 1. Specimen CCB.2.Kgi.1; 2. specimen 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 wagneri* (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.

its paleobiogeographical 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 classic British, German and Normandian *Leptaena* beds (Deslongchamps, 1853; Davidson, 1876–1878; Rau, 1905; Ager, 1990), and *Koninckella* faunas recorded in France, Portugal and Morocco (Almérás et al., 1988; Almérás and Fauré, 1990; Almérás 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.

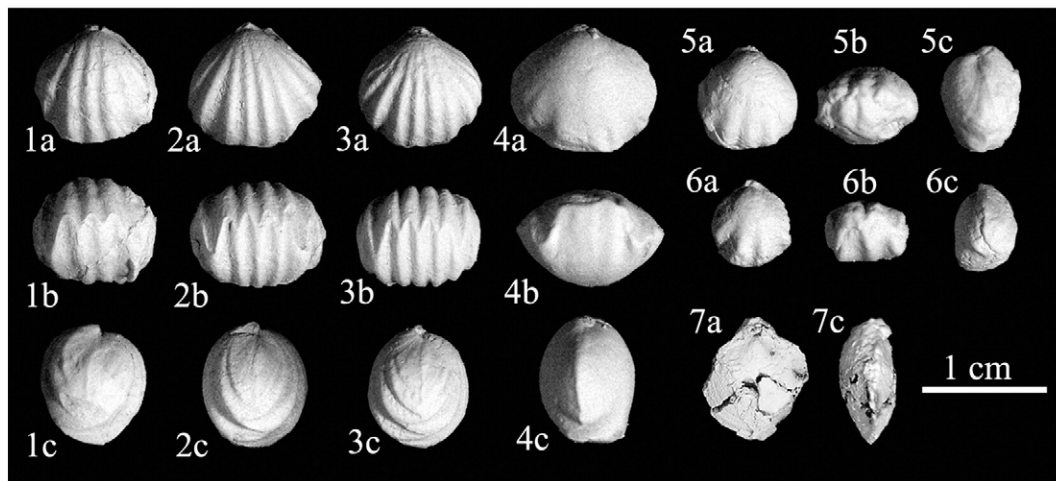


Fig. 4. Some representative taxa associated to the koninckinid fauna from the easternmost Subbetic area (a: dorsal, b: anterior, and c: lateral views). All specimens were coated with magnesium oxide. 1–3. *Nannirhynchia pilulla* (Schlosser in Böse and Schlosser) from JdC collection. 1. Specimen O.VIII.23.5; 2. Specimen O.IV.1.T2.3; 3. Specimen O.IV.1.T2.4. 4. *Nannirhynchia* aff. *gemmellari* (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.

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 epicenean swells, coexist with sulcate and smooth terebratulids (*Linguithyris*, *Viallithyris*, *Rhaphidothyris*), 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 a 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 echinoid 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 sulfides (Figs. 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

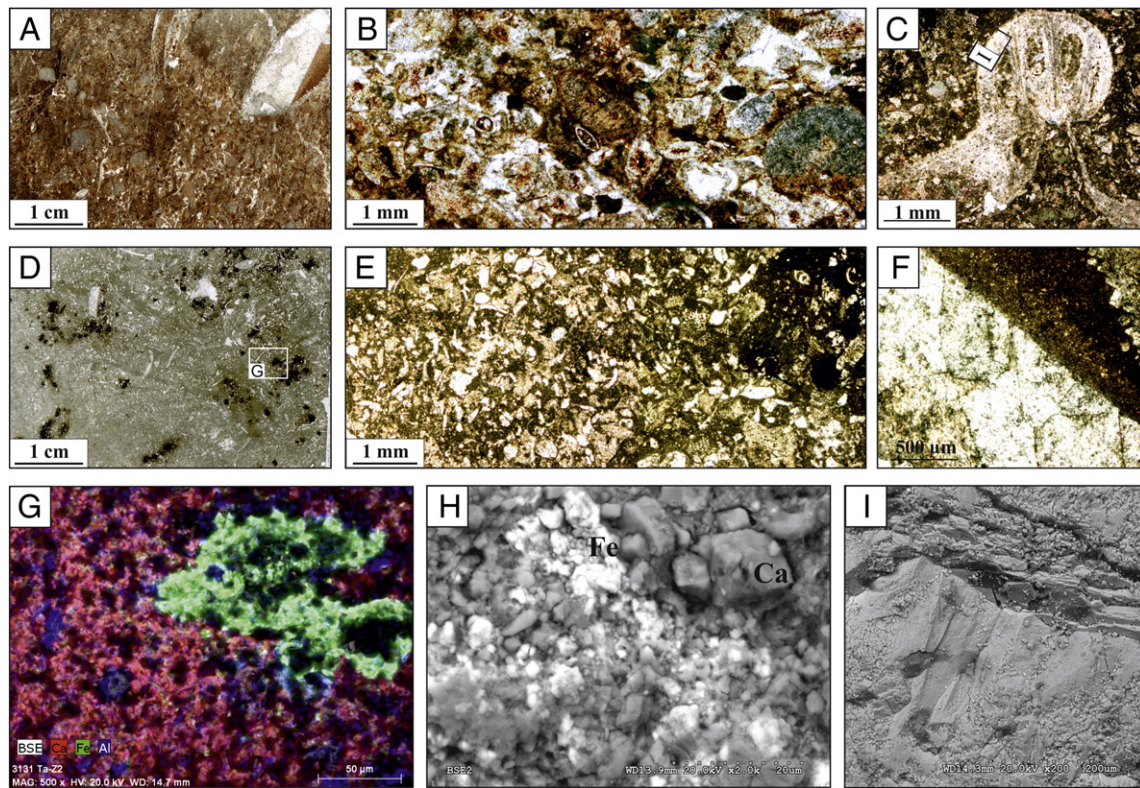


Fig. 5. Microfacies photographs and SEM EDX-mapping aimed at the analysis of the oxide composition. A–C. Crinoidal packstone microfacies. A. Polished slab; B. microfacies photograph, C. detail of spiriferinid-section (ventral valve in the upper part). D–F. Marly limestone microfacies. Note the presence 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 shown in C, noting details of the shell microstructure and calcite layers.

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 *Calliphylloceras bicicola*, *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*, *Catuloeloceras*, *Osperleioceras*, *Phymatoceras*, *Pseudolillia*, *Hildoceras*, *Catulloeloceras*, and *Graphoceras* gr. *concavum*, therefore including chronorecords from the lower Toarcian to the Aalenian (Iñesta, 1988; Caracul et al., 2004).

In the Tarabillo and Sierra de Orts sections (Fig. 2), condensed levels with *Fuciniceras portisi*, *Fuciniceras lavinianum* and *F. isseli* underlie the koninckinid beds. These levels were attributed to the basal upper Pliensbachian (Lavinianum Zone, Portisi Subzone) by Braga (1983); Baeza-Carratalá (2013). In addition, koninckinids in these outcrops are recorded together with some constituents of a brachiopod assemblage (e.g. *Liospiriferina? undulata* and *L. 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 *Parhabdolit* sp. Likewise, some constituents of the koninckinid beds have been recorded in La Alguada 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 *O. 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).

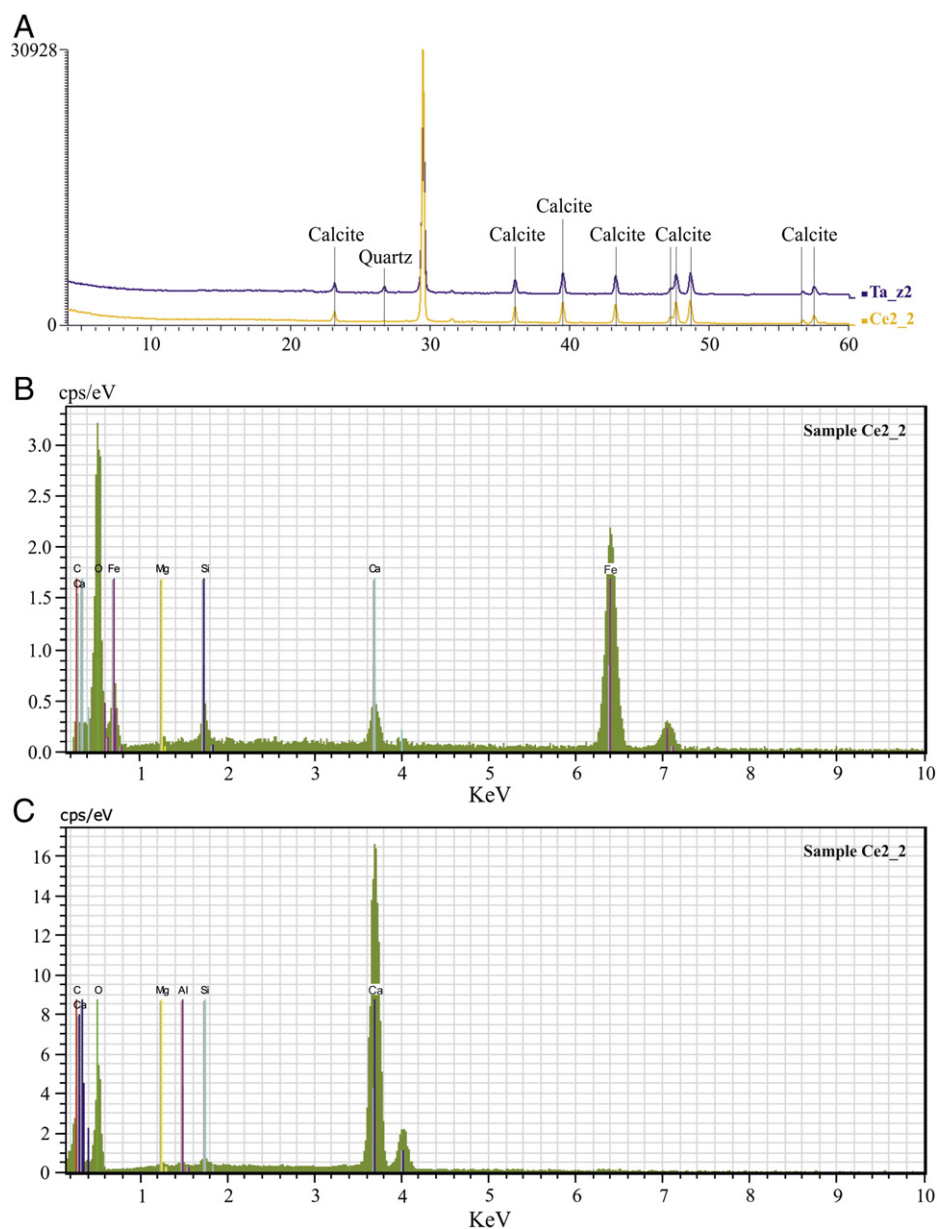


Fig. 6. A. Mineralogical composition of different koninckinid-bearing levels performed on both crinoidal grainstone (Ta.ZZ.Pi) and calcareous sandy marlstone (CC.2.2.pi) powdered samples by X-RD. B–C. Geochemical microanalysis performed under SEM with energy dispersive X-ray spectrometry (EDS) on (B)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

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.ZZ.pi: sample of calcareous sandy marlstone from Tarabillo section. LOI: loss on ignition.

Elements (%)			Oxides (%)		
	CC-2-2-pi	Ta-ZZ-pi		CC-2-2-pi	Ta-ZZ-pi
Ca	40.2	33.1	MgO	0.534	0.627
O	18.7	23.5	Al ₂ O ₃	0.951	1.912
Si	1.38	6.67	SiO ₂	2.947	14.262
Fe	0.583	2.82	P ₂ O ₅	0.122	0.205
Al	0.503	1.01	SO ₃	0.063	0.089
Cl	0.38	0.5	K ₂ O	0.179	0.54
Ba	0.349	–	CaO	56.182	46.317
Mg	0.322	0.378	Fe ₂ O ₃	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 ₂		0.141
Sr	<<	0.0189	Cl	0.38	0.5
Cu	–	<<	LOI	37.42	31.36
Ti	–	0.0843			

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 (*K. bolivari*, *K. gibbosula*, *K. fornicata*, *K. waehneri*, *K. davidsoni*, *K. styriaca* (?), *N. reynesi*, *N. gemmellaroii*, *G. cf. orsinii*, *C. briseis*, *Linguithyris aspasia*, *Antiptychina? rothpletzi*, and *Liospiriferina alpina*). This assemblage was tentatively assigned to the earliest Toarcian by Vörös (2003),

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 remobilization, 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 Domerian 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 grypheid 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 koninckinid 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. Almérás 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, Vörös (2002) ascertained that the paleogeographical 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 for 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 epiocenic–epicontinental habitats either via the Lusitanian Basin or via the Laurasian Seaway (sensu Bjerrum et al., 2001; Vörös, 2002).

In this sense, the easternmost Subbetic basin was the westernmost Tethyan area where the koninckinid fauna is recorded in a clearly oxygen-rich epiocenic 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; Almérás 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 toward 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 searoom 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 *N. reynesi*, *N. gemmellaroi*, *N. pilulla* and related forms recorded in epiocenic 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 *K. davidsoni* in the Atlantic basins). In addition, the supraspecific taxonomical attributions recorded

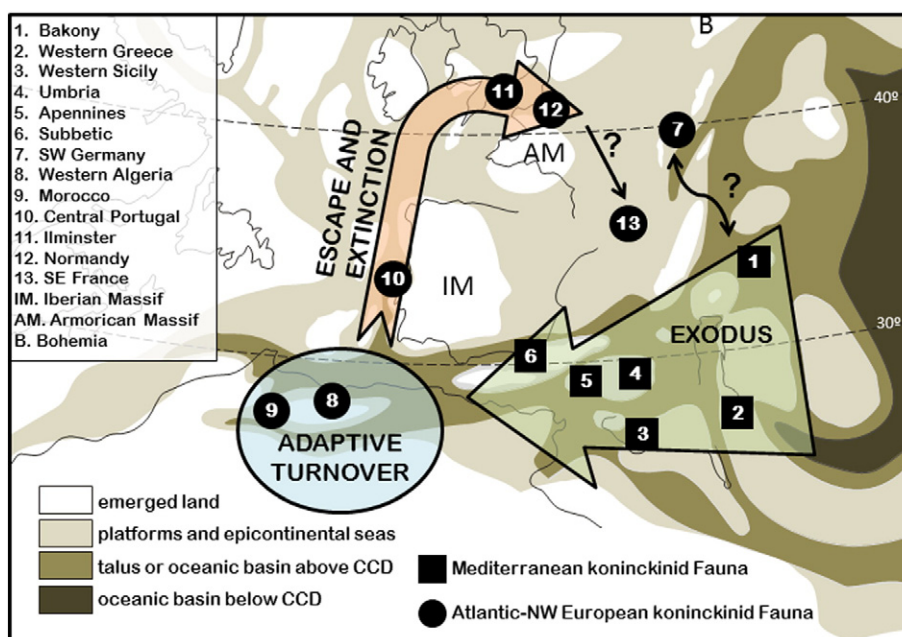


Fig. 7. Paleogeographical map of the late Pliensbachian–earliest Toarcian (slightly modified after Bassoullet et al., 1993), showing representative westernmost Tethyan localities with koninckinid fauna records (sources cited in the text) and the main evolution phases suggested. Records from Mediterranean well-oxygenated habitats and those from the epicontinental NW-European areas have been distinguished. Tentative connections or unreliable data are marked with a (?).

in the koninckinid fauna (*Nannirhynchia*, *Koninckella*, *Koninckodonta*, *Orthotoma*) seem 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 paleobiogeographical 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 $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ fluctuations, often correlated with manifest bioevents. Paleotemperatures 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 (García Joral et al., 2011; Gómez and Goy, 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 $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values connected with biotic events

in the Polymorphum–Serpentinum interval. Such studies also deduced significant paleotemperature 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 $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ 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 *L. arcta* or *L. 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,

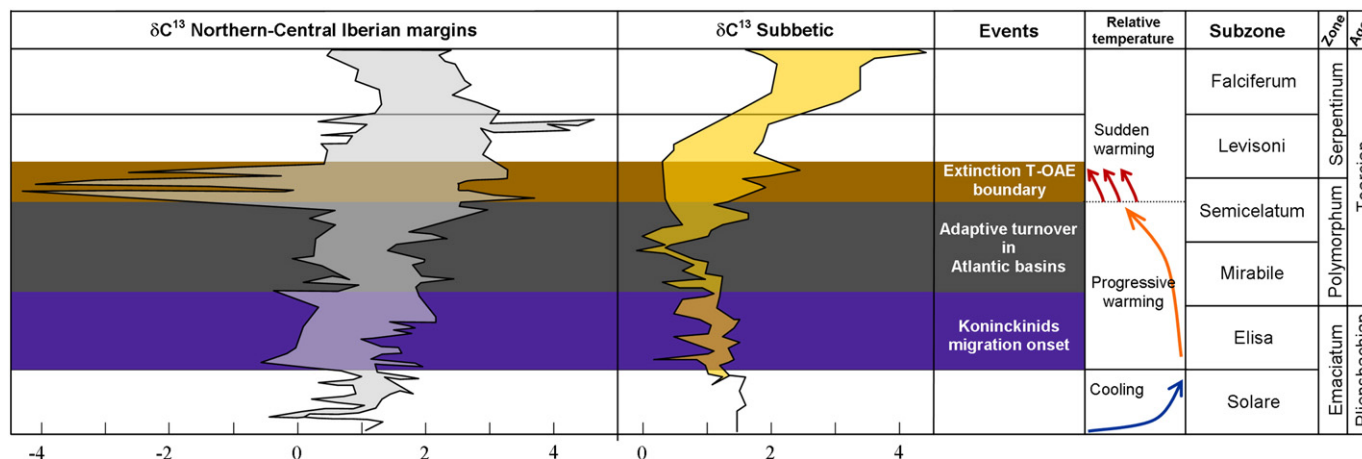


Fig. 8. Correlation sketch showing the relationship between koninckinid fauna events inferred, isotopic $\delta^{13}\text{C}$ fluctuations and relative paleotemperature variations around the Subbetic and Northern-Central Iberian marginal platforms. Outline enveloping curves enclosing the main $\delta^{13}\text{C}$ values and deviations and paleotemperature data are based on García Joral et al. (2011); 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.

1993; Vörös, 2003, 2009) toward the Western Tethys regions (Vörös, 2002). They found a suitable habitat to colonize in the easternmost Subbetic (sensu Vörös, 2002), dominated by epiocenic 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 *N. reynesi*, *N. gemmellaro*, *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 *K. liasiana* with only scarce large-sized *K. 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 classic 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 epiocenic seamounts are also confirmed by Gischler et al. (2003) or Little et al. (2004).

6.5.2. Paleontological proxies

Gregarious behavior 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 epiocenic 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; Baeza-Carratalá et al., 2011; García Joral 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; Kaim et al., 2013; Kiel 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 $\delta^{13}\text{C}$ 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 paleotemperatures 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 paleobiogeographically consistent with the course of the previously well-established clockwise migration route toward 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:

- 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 epiocenic 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 paleogeographic 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 noticeable only 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.

Acknowledgments

This research is a contribution to the projects CGL2011-25894 and CGL2011-23947 (Ministry of Science and Innovation, Government of Spain) and to the Research Group VIGROB-167 (University of Alicante). Authors are deeply grateful to Dr. C. Lancis (University of Alicante) for the substantial help with the classification and analysis of calcareous nannoplankton and to Dr. J. Martínez and Dr. D. Benavente (University of Alicante) for their support in petrographical and geochemical analysis. We gratefully acknowledge Editor F. Surlyk, and reviewers M.O. Manceñido, A. Vörös and another anonymous reviewer for their valuable comments and constructive reviews. Kate Burke helped to improve the English text.

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