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Response of Lower Toarcian (Lower Jurassic) macrobenthos of the Iberian Peninsula to sea level changes and mass extinction

Cambios del nivel del mar y extinción en masa: la respuesta de la fauna bentónica en el Toarciense Inferior (Jurásico Inferior) de la Península Ibérica

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Abstract

Palaeoecological analysis of Lower Toarcian benthic faunas from the Lusitanian Basin (Portugal) and the Celtiberian Chains (Spain), combined with a sequence stratigraphic interpretation, enables to document the close correlation between environmental parameters, such as substrate stability and food supply, and sea level changes. As these environmental parameters remained more or less constant in a given environment for a long geologic time, the faunal communities controlled by these factors can be compared with similar communities of a different geologic age.

Apart from the environmental parameters, also biological factors contributed to the composition and distribution of the benthic fauna, especially during the Early Toarcian mass extinction. It is shown that amongst these biological factors the number of competitive taxa is one of the most important. If this number is low, opportunists can rapidly spread over a large area. If this number is high, increased biological stress can lead to unstable conditions and frequently changing faunal compositions.

Only in the lowermost Toarcian (*tenuicostatum* Zone) the composition and distribution of the benthic fauna of the Lusitanian Basin and the Celtiberian Chains was controlled by environmental parameters, whilst in the Upper Toarcian (*serpentinum* Zone) biological parameters predominated.

Keywords: palaeoecology, benthic communities, sequence stratigraphy, mass extinction, Lower Toarcian, Iberian Peninsula

Resumen

La combinación de un análisis paleoecológico de faunas bentónicas del Toarciense Inferior de la Cuenca Lusitánica (Portugal) y la Cordillera Ibérica (España) con un análisis de la secuencia estratigráfica muestra la conexión íntima entre parámetros ambientales, como estabilidad del sustrato y suministro de nutrientes, y cambios del nivel del mar. Como estos parámetros ambientales en un ambiente determinado se mantienen mas o menos constantes durante el tiempo geológico, las comunidades faunísticas que estuvieron controladas por estos parámetros pueden ser comparadas con comunidades similares de de diferentes edades geológicas.

Además de los parámetros ambientales, también parámetros biológicos tienen influencia sobre la composición y la distribución de la fauna bentónica, especialmente durante la extinción masiva del Toarciense Inferior. Puede apreciarse como entre estos parámetros biológicos uno de los más importantes es el número de taxones competitivos, pues si este número es pequeño, aquellos oportunistas pueden extenderse rápidamente sobre un área enorme, mientras que, si este número es grande, el estrés biológico creado puede producir condiciones de inestabilidad y cambios frecuentes en las composiciones de la fauna.

La composición y la distribución de la fauna bentónica de la Cuenca Lusitánica y la Cordillera Ibérica está controlada por parámetros ambientales sólo en el Toarciense más bajo (Zona *Tenuicostatum*), mientras que en la parte superior del Toarciense (Zona *Serpentinum*) los parámetros biológicos son los que predominan.

Palabras clave: paleoecología, comunidades bentónicas, secuencia estratigráfica, extinción en masa, Toarciense Inferior, Península Ibérica

1. Introduction

Numerous palaeoecological analyses (e.g. Aberhan, 1992; Fürsich, 1977; Fürsich and Werner, 1986; Fürsich and Oschmann, 1990; Fürsich *et al.*, 1991; Heinze, 1991; Holzapfel, 1998) documented a strong relationship between the fossil macrobenthos and environmental parameters. This has also been demonstrated for the macrobenthic associations occurring in the Lower Toarcian of the Iberian Peninsula (Gahr, 2002).

As these environmental parameters are affected by sea-level changes, it should be possible to correlate the associations with documented transgressive and/or regressive trends.

1.1. Study area

During field work for a palaeoecological analysis of Lower Toarcian (Lower Jurassic) macrobenthic faunas of the Iberian Peninsula (Gahr, 2002) five sections have been investigated in detail (Fig. 1).

In the Lusitanian Basin (Portugal) the Maria Parès section (Z, Fig. 2D) near Zambujal and Rabaçal has been studied (e.g. Mouterde *et al.*, 1964; Hallam, 1971; Duarte and Soares, 1993; Duarte, 1994; 1997a; 1997b; 1998).

Due to better outcrop conditions in the Celtiberian Chains (Spain) four sections could be investigated: the La Almunia de Doña Godina section (AL, Fig. 2B; e.g. Martínez, 1986; Goy *et al.*, 1996), and three up to now unknown localities near Obón (Barranco de Santa María section, SA, Fig. 2C) and in the Montes Universales near Albarracín (Barranco de la Cañada section, C, and Barranco de la Masía section, MA, Fig. 2A).

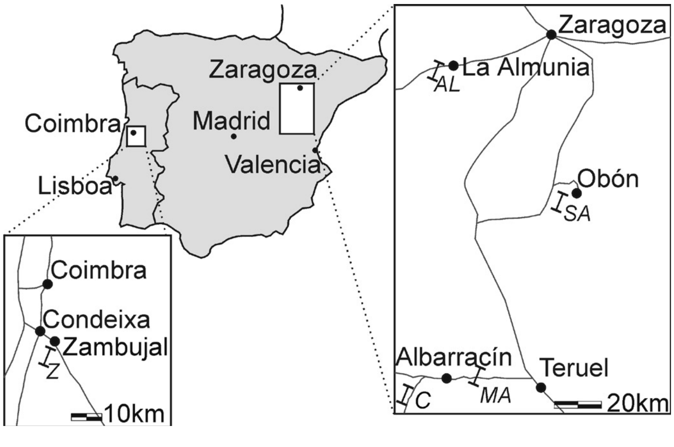


Fig. 1.–Geographic positions of the sections in Spain and Portugal (modified after Gahr, 2002).

Fig. 1.–Posición geográfica de las localidades en España y Portugal (modificada de Gahr, 2002).

1.2. Geological framework

1.2.1. Palaeogeography

In the Lower to Middle Toarcian, the study areas were situated on the middle to lower shelf, to the west (Lusitanian Basin) and to the east (Celtiberian Basin) of the Iberian Massive (Fig. 3). Whilst in the Celtiberian Basin the shelf was developed as a gently sloped homoclinal ramp (e.g. Villena *et al.*, 1971; Comas-Rengifo *et al.*, 1996; Gahr, 2002), in the Lusitanian Basin the homoclinal ramp was probably steeper and more strongly influenced by tectonic activity (Alméras and Elmi, 1993; Duarte and Soares, 1993; Stapel *et al.*, 1996; Kullberg *et al.*, 2001). In the Celtiberian Basin the inferred water depth based on some faunal elements was about 40-70 m on average (Gahr, 2002). Due to higher rates of subsidence (Duarte and Soares, 1993; Stapel *et al.*, 1996), the water depth in the Lusitanian Basin might have been slightly deeper (about 80-120 m on average). In both basins it was most of the time below storm wave base.

1.2.2. Lithostratigraphy

For the Toarcian of the Celtiberic Chains Behmel and Geyer (1966) and Mensink (1966) were the first to establish lithostratigraphic units. As they misidentified some Toarcian ammonites (Dubar *et al.*, 1970) also the names of their lithostratigraphic units became incorrect (Gahr, 2002). Therefore, the lithostratigraphic units of Goy *et al.* (1976) seem to be more appropriate, even though they differentiated "members" by colors that cannot be recognized in most sections (Fig. 4).

For the section in the Lusitanian Basin, Duarte (1994) established appropriate lithostratigraphic units. However, for the lowermost marls of the Toarcian ("Margo-Calcários com Fácies de *Leptaena*", e.g. Duarte, 1994; Duarte and Soares, 2002; Duarte *et al.*, in press) he accepted an older identification of a common athyridid brachiopod as "*Leptaena*", which is quite misleading. To avoid confusion with the Palaeozoic brachiopod species, the name proposed by Alméras *et al.* (1988) and Alméras and Elmi (1993) i.e. "Margo-Calcários com Fácies de *Koninckella*", which is based on a more recent classification of the brachiopod, should be preferred (Fig. 4).

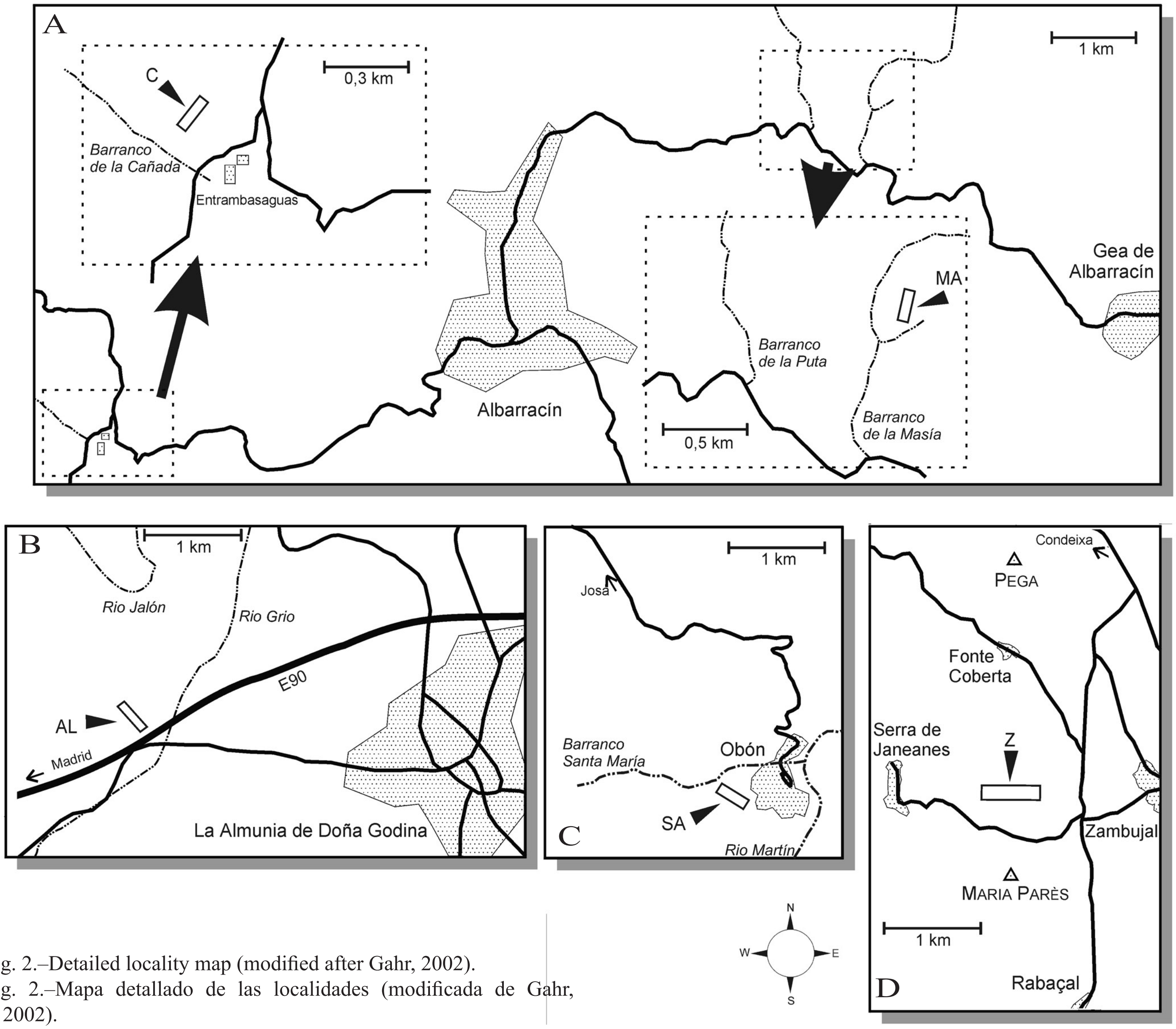


Fig. 2.–Detailed locality map (modified after Gahr, 2002).
Fig. 2.–Mapa detallado de las localidades (modificada de Gahr, 2002).

1.2.3. Biostratigraphy

In the case of the Spanish sections, well preserved ammonites that could serve for biostratigraphic purposes are rare. Nevertheless, using foraminifera (e.g. Herrero, 1991; 1993; 1994) in combination with brachiopods (e.g. Goy, 1974; Goy *et al.*, 1984; García-Joral and Goy, 2000) a biostratigraphic zonation can easily be established (Fig. 4). However, following Martínez (1986), Goy and Martínez (1990) and Goy *et al.* (1996), in the La Almunia section (AL) spiriferids are present up to 2 m above the base of *serpentinum* Zone and the *Soaresirhynchia* Beds appear 3 m above this boundary. The nearly monospecific layers of the rhynchonellid brachiopod *Soaresirhynchia* typically occur only few centimeters to decimeters above the base of the *serpentinum* Zone even outside the basin (e.g. in Morocco: Rousselle, 1975; Alméras, 1993; Algeria: Alméras and Elmi, 1993; Hungary: Vörös, 1993). Together with the observation that in all of the other localities described herein spiriferids occur only up to the top of the *tenuicostatum* Zone, it is very likely that in this section the boundary between *tenuicostatum* and *serpentinum* Zone is drawn about 2 m too low, and therefore has to be corrected (Gahr, 2002).

In most parts of the Maria Parès section (Z) of the Lusitanian Basin, ammonites are abundant, but the first description of the sediments by Mouterde *et al.* (1964) bears some errors (Gahr, 2002). The biostratigraphy has been corrected according to Duarte and Soares (1993) and (Duarte (1994).

2. Sequence Stratigraphy

Although many studies of Spanish workers of the last years e.g. Goy *et al.* (1996) and Comas-Rengifo *et al.* (1996; 1997) include sequence stratigraphic interpreta-

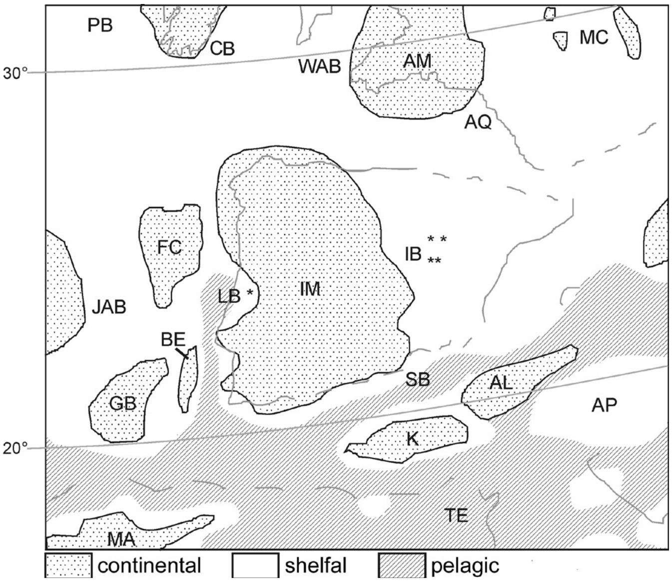


Fig. 3.–Palaeogeographic map of SW-Europe during the Middle Toarcian (modified after Dommergues and Mouterde, 1987, Bassoullet *et al.*, 1993 and Gahr, 2002); An asterisk marks the position of the sections. Abbreviations: AM: Armorican Massif, AL: Alboran Block, AP: Appeninic Platform, AQ: Aquitaine Basin, BE: Berlengas Block, CB: Celtic Basin, FC: Flemish Cap, GB: Galician Bank, IB: Iberian Basin, IM: Iberian Meseta, JAB: Jeanne d'Arc Basin, K: Kabylia, LB: Lusitanian Basin, MA: Middle Atlas, MC: Massif Central, PB: Porcupine Basin, SB: Subbetic Basin, TE: Tethys, WAB: Western Approaches Basin.

Fig. 3.–Mapa paleogeográfico del SW de Europa en el Toarciense Medio (modificada de Dommergues y Mouterde, 1987, Bassoullet *et al.*, 1993 y Gahr, 2002); * marca la posición de las localidades.

tions of single sections, a synopsis of these results is lacking so far. Such a summary e.g. in form of a traverse from the ramp to the basin can provide new data for the interpretation of the sedimentary environments.

However, such a synopsis is beyond the scope of this paper, and as in most of the above mentioned publications no quantitative data for the benthic faunas are given, these papers do not contribute to the ecological interpretation of the sedimentary environment.

For the Lusitanian Basin sequence stratigraphy has already been carried out for the Maria Parès section (Z) near Rabaçal (Duarte, 1997a; 1997b; 1998). To avoid confusions with the sequences, which he called "mesosequences", this paper follows the nomenclature of van Wagoner *et al.* (1988) (Table 1). The abbreviations used in the following text and figures are explained in Table 2.

Especially in the Lower Toarcian, depositional sequences can be determined accurately (Figs. 5 and 6) and correlated with the results of Duarte (1997a; 1997b; 1998; see Table 1 and Fig. 5 for his terms) and Hardenbol *et al.*, (1998). The recognized sequence boundaries (SB) and depositional sequences (DS) are as follows (Fig. 6):

van Wagoner *et al.* (1988)	-	Duarte (1997a; 1997b; 1998)
depositional sequence	-	*mesosequence*
parasequence set	-	*macrosequence*
parasequence	-	*elementary sequence*

Table 1.–Comparison of the nomenclatures of van Wagoner *et al.* (1988) and Duarte (1997a; 1997b; 1998), modified from Duarte (1997a) and Gahr (2002).

Tabla 1.–Comparación de las nomenclaturas de van Wagoner *et al.* (1988) y Duarte (1997a; 1997b; 1998), modificada de Duarte (1997a) y Gahr (2002).

(1) Sequence boundary Tc 1: Duarte (1997a; 1997b) designated this boundary as DT1 (D for discontinuity, T for Toarcian). As he pointed out, this boundary at the top of the Pliensbachian/base of the Toarcian is isochronous throughout the Lusitanian Basin.

Even in the Celtiberian Basin this boundary is developed as a discontinuity (type-I hardground *sensu* Fürsich, 1979) with omission or very low sedimentation rates (Gahr, 2002). As the development of this discontinuity reflects a very strong transgressive pulse most likely this boundary is isochronous in both basins.

(2) Depositional sequence Tc 1: Duarte (1997a; 1997b) determined this sequence as MST1 (MS for mesosequence, T for Toarcian) which, in his opinion, spans the hole *tenuicostatum* Zone as an independent megasequence (ME1). The predominantly marly sediments of the *Margo-Calcários com "Fácies de Koninckella"* in this interval reflect a deepening phase (Duarte, 1997a; 1997b).

Even in the Celtiberian Chains, the depositional sequence Tc 1 can be recognized (Goy *et al.*, 1996; Gahr,

DS	*depositional sequence* The name of a sequence is build up by a combination of DS Tc (Tc for Toarcian) and the serial number.
HST	*highstand systems tract*
LST	*lowstand systems tract*
mfz	*maximum flooding zone* Named as an interval as it is not possible to make out a determined layer as *maximum flooding surface.*
SB	*sequence boundary* The name of a sequence boundary is build up by a combination of SB Tc (Tc for Toarcian) and the serial number.
ts	*transgressive surface*
TST	*transgressive systems tract*

Table 2.–Explanation of the abbreviations used in the text and figures; modified from Gahr (2002).

Tabla 2.–Explicación de las abreviaciones usadas en el texto y en las figuras; modificada de Gahr (2002).

	zones	subzones	Celtiberian Chains		Lusitanian Basin
Toarcian	*Hildoceras bifrons*	*Hildoceras semipolitum*	Formación Alternancia de Margas y Calizas de Turmiel *(Fm. Turmiel)*	Miembro Alternancia rítmica de Margas y Margocalizas	Margas e Calcários do Moinho
		Hildoceras bifrons			
		Hildoceras sublevisoni		Miembro Margas rojas	
	Harpoceras serpentinum	*Harpoceras falciferum*		Miembro Calizas amarillas y Margas verdosas	
		Harpoceras strangewaysi			Calcários em Plaquetas
	Dactylioceras (Orthodactylioceras) tenuicostatum	*Dactylioceras (Orthodactylites) semicelatum*		Miembro Margas y Calizas Margosas	Margo-Calcários com "Fácies de Koninckella"
		Dactylioceras (Eodactylites) mirabile			
Pliens-bachian	*Pleuroceras spinatum*	*Pleuroceras hawskerense*	*Fm. Barahona*		

Fig. 4.–Biostratigraphy and lithostratigraphy of the Lower Toarcian of the Celtiberian Chains (Goy *et al.*, 1976) and the Lusitanian Basin (based on Duarte, 1994 - see Fig. 5).

Fig. 4.–Bioestratigrafía y litoestratigrafía del Toarciense Inferior de la Cordillera Ibérica (Goy *et al.*, 1976) y la Cuenca Lusitánica (basado en Duarte, 1994 - *vide* Fig. 5).

2002). As in the Lusitanian Basin, it consists of predominantly marly sediments showing a retrograde development of the sedimentary environment. This sequence has also been recognized by Hardenbol *et al.* (1998), even though the maximum flooding zone of this depositional sequence of Gahr (2002) falls already in the higher *mirabile* Subzone.

(3) Sequence boundary Tc 2: According to Duarte (1997a; 1997b - herein designated as DT2) this sequence boundary marks the boundary between *tenuicostatum* and *serpentinum* Zone and between MST1 and MST2. At some localities within the Lusitanian Basin it forms an erosional surface. Goy *et al.* (1996) described this sequence boundary from the same level in the La Almunia section (AL) as discontinuity marked by an iron-bearing crust. However, during his field work Gahr (2002) could not find this crust. Here, the sequence boundary Tc 2 is placed already in the *semicelatum* Subzone due to the striking similarity in lithology with that of the other sections (SA, C and MA). As mentioned above, in the Maria Parès section (Z) the sequence boundary marks the base of the *serpentinum* Zone (Duarte, 1997a; 1997b). However, most parts of the following *Calcários em Plaquetas* are unfossiliferous and thus the precise biostratigraphic zonation is not known. It is therefore conceivable that even in the section of the Lusitanian Basin the sequence boundary falls within the *semicelatum* Subzone.

The same could be true of the La Almunia section (AL): As pointed out by Gahr (2002), the base of the *serpentinum* Zone has been placed about 2 m too low by former authors (e.g. Martínez, 1986; Goy *et al.*, 1996). The position of the sequence boundary Tc 2 within the *semicelatum* Subzone, therefore, seems most likely. These results are in accordance with the data of Hardenbol *et al.* (1998), whose Toa1 can be correlated with the sequence boundary Tc 2 in this interval.

(4) Depositional sequence Tc 2: In the Maria Parès section (Z) this sequence starts with the *Calcários em Plaquetas* which, according to Duarte (1997a; 1997b), are the basal part MST2A of the mesosequence MST2 and document eustatic sea level fall. However, as explained above parts of the *Calcários em Plaquetas* most likely still belong to the depositional sequence Tc 1 and document shallow water during the middle to higher highstand systems tract. Only in the upper parts of the *Calcários em Plaquetas* progradation is documented by slightly increasing thickness of the layers. Likewise, Bucefalo Palliani *et al.* (1998) and Prauss (1996) describe sequences with the maximum flooding zone in the upper part of the *tenuicostatum* Zone. It seems likely, that this sequence

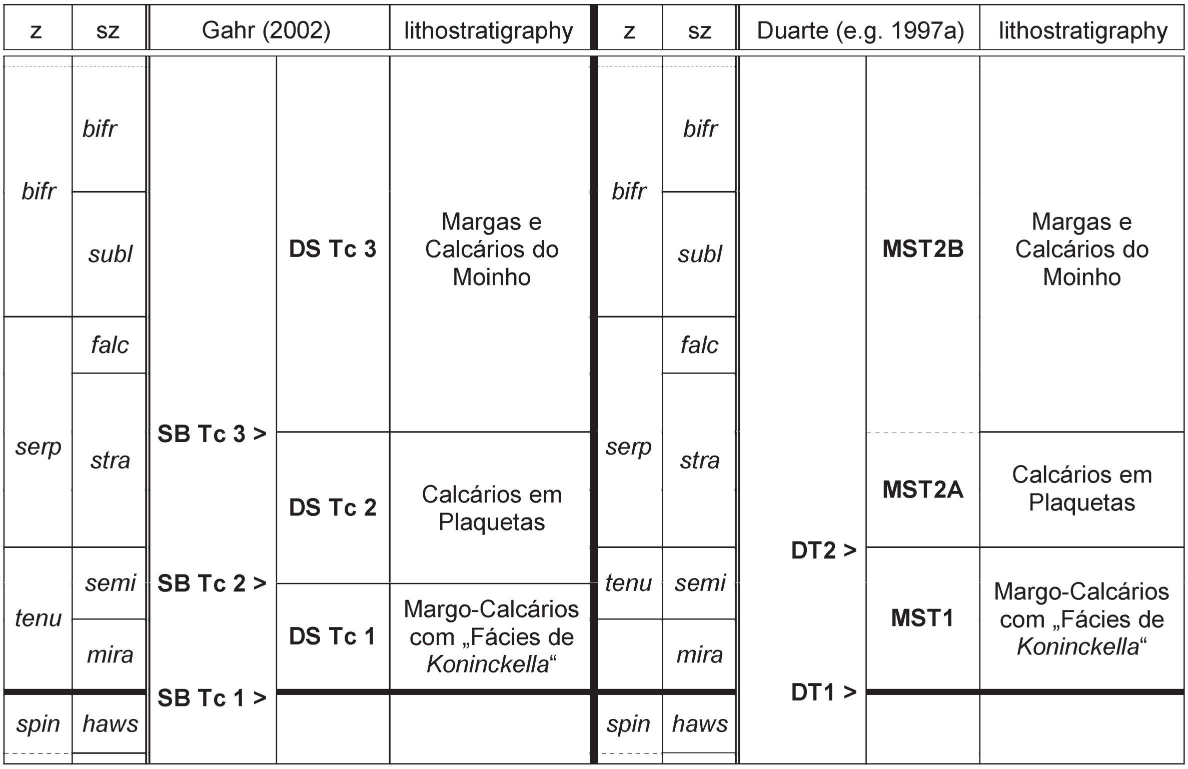


Fig. 5.–Comparison of the sequence stratigraphic interpretations of the Maria Parès section (Z) by Gahr (2002) and by Duarte (1997a; 1997b; 1998). Sequence boundaries Tc 1 to 3 and depositional sequences Tc 1 to 3 are also well be seen in the sections of the Celtiberian Basin; modified after Gahr (2002). Abbreviations of the biostratigraphic zones (z) and subzones (sz): *spin = spinatum, tenu = tenuicostatum, serp = serpentinum, bifr = bifrons*; *haws = hawskerense, mira = mirabile, semi = semicelatum, stra = strangewaysi, falc = falciferum, subl = sublevisoni, bifr = bifrons*.

Fig. 5.–Comparación de las interpretaciones de la sequencia estratigráfica de la sección Maria Parès (Z) según Gahr (2002) y según Duarte (1997a; 1997b; 1998). Se puede reconocer las límites sequence boundary Tc 1 a 3 y las unidades depositional sequence Tc 1 a 3 tambien en las localidades de la Cordillera Ibérica; modificada de Gahr (2002).

can be correlated with the depositional sequence Tc 2.

(5) Sequence boundary Tc 3: In the Celtiberic sections this sequence boundary in the lower *serpentinum* Zone is documented by bioclastic carbonates (rudstones), tempestites and occasional wood fragments indicating a low sea level. In the Lusitanian Basin this sequence boundary is only marked by a few layers with more bioclasts. Therefore, this sequence boundary was not recognized by Duarte (1997a). In his opinion the transition from his MST2A to his MST2B is gradual. In contrast, even Hardenbol *et al.* (1998) document a sequence boundary in the lower *serpentinum* Zone (Toa2), which can be correlated with the sequence boundary Tc 3.

(6) Depositional sequence Tc 3: As already mentioned, in the opinion of Duarte (1997a) the change from the MST2A to the following carbonate-marl alternations of the *Margas e Calcários do Moinho* is gradual. As no sequence boundary is documented, these sediments represent the upper part of the same sequence (MST2B), which according to him first shows a transgressive, later a regressive trend.

However, in the Spanish sections the well defined sequence boundary Tc 3 documents the base of a distinct DS, beginning with a characteristic pattern of parasequence sets in all of the sections (Gahr, 2002). These patterns are interpreted as sediments of aggradation to slight progradation during the lowstand systems tract. A transgressive surface can only be found in the Barranco Santa María section (SA).

In this paper, Middle Toarcian rocks (higher *serpentinum* Zone, *bifrons* Zone) were studied only in the Maria Parès section (Z) and the Barranco de la Cañada section (C). At the present state of knowledge, a sequence stratigraphic correlation of the two sections located in different basins is tentative (Gahr, 2002).

3. The benthic fauna

3.1. Methods and composition of the benthic fauna

The Lower Toarcian rocks of the sections were studied in detail and their macrofaunal content was sampled bed-by-bed. This investigation yielded 563 samples with about 20.000 macrobenthic fossils in total, which could be assigned to 183 taxa (Gahr, 2002). The composition of the fauna is shown in Figure 7.

Various environmental parameters were reconstructed based on a palaeoecological analysis of the benthic macrofauna (Gahr, 2002). For this purpose, after identification of the fauna, lists of relative abundances were constructed for each quantitative sample. In the case of bivalves and brachiopods the number of individuals was obtained by adding to the number of articulated specimens the number of right or left valves (pedicle and brachial valves in the case of brachiopods), whichever was larger ["Minimum Number of Individuals (MNI)-method" according to Gilinsky and Bennington, 1994]. Due to their high degree of disarticulation, crinoids were excluded from the quantitative palaeoecological analysis.

To establish benthic associations, a Q-mode cluster analysis was carried out using the program SPSS for Windows. Calculations were based on the Ward method to obtain homogeneous clusters. For this cluster analysis, only samples with more than 35 individuals, regarded as statistically significant in the present case, were used (144 samples with about 12.000 individuals from 177 taxa in total). The cluster analysis allowed the distinction of 32 independent community relicts (10 faunal associations, 17 subsets of associations and 5 faunal assemblages, *sensu* Fürsich, 1984), dominated by bivalves and brachiopods (Table 3).

In addition, species diversities of the established statistical units were expressed by the number of species (species richness) and evenness values, the latter calculated according to the formula of MacArthur (1972).

3.2. Influences on the benthic fauna from SW-Europe

3.2.1. Faunal community relicts at the sequence boundary and in the lowermost transgressive systems tract

Of all the sequence boundaries in the Lower Toarcian, only the sequence boundary Tc 1 (at the base of the Toarcian) is, as mentioned above, well developed as a hiatal type-I hardground. Only a scarce fauna is associated with this hardground such as some big pholadomyid bivalves which - most likely due to their strength - were able to burrow deeply in the already firm substrate (Di Celma *et al.*, 2002), and a few cementing oysters. As in all sections at this boundary faunal elements are generally rare, the fauna was excluded from quantitative methods such as diversity measurement and cluster analysis.

Brachiopod-dominated (17 communities: 53,1 %)

associations
- *Homoeorhynchia meridionalis* ssp. A - association
- *Homoeorhynchia meridionalis batalleri* - association
- *Liospiriferina rostrata* - association
- *Liospiriferina undulata* - subset
- *Lobothyris arcta* - *Liospiriferina undulata* - subset
- *Lobothyris hispanica* - association
- *Nannirhynchia* - *Plicatula spinosa* - subset
- *Soaresirhynchia* - HD-subset
- *Soaresirhynchia* - LD-subset
- *Telothyris jauberti* - association
- *Telothyris pyrenaica* - association

assemblages
- *Homoeorhynchia meridionalis meridionalis* - assemblage
- *Lobothyris subpunctata* - subset
- *Sphaeroidothyris perfida* - subset

Bivalve-dominated (12 communities: 37,5 %)

associations
- *Corbulomima* - association
- *Cucullaea* - association
- *Gryphaea* cf. *sublobata* - HD-subset
- *Gryphaea* cf. *sublobata* - LD-subset
- *Gryphaea* cf. *dumortieri* - Katosira - subset
- *Homomya* cf. *alsatica* - HD-subset
- *Homomya* cf. *alsatica* - HD-subset
- *Plicatula spinosa* - *Dorsoserpula* sp. - subset
- *Plicatula spinosa* - *Liospriferina villosa* - subset

assemblages
- *Bositra buchi* - assemblage
- *Palaeoneilo* - assemblage
- *Parvamussium pumilum* - assemblage

Coral-dominated (2 associations: 6,4 %)

- *Montlivaltia* - association
- *Montlivaltia* - *Telothyris pyrenaica* - association

Gastropod-dominated (1 association: 3,1 %)

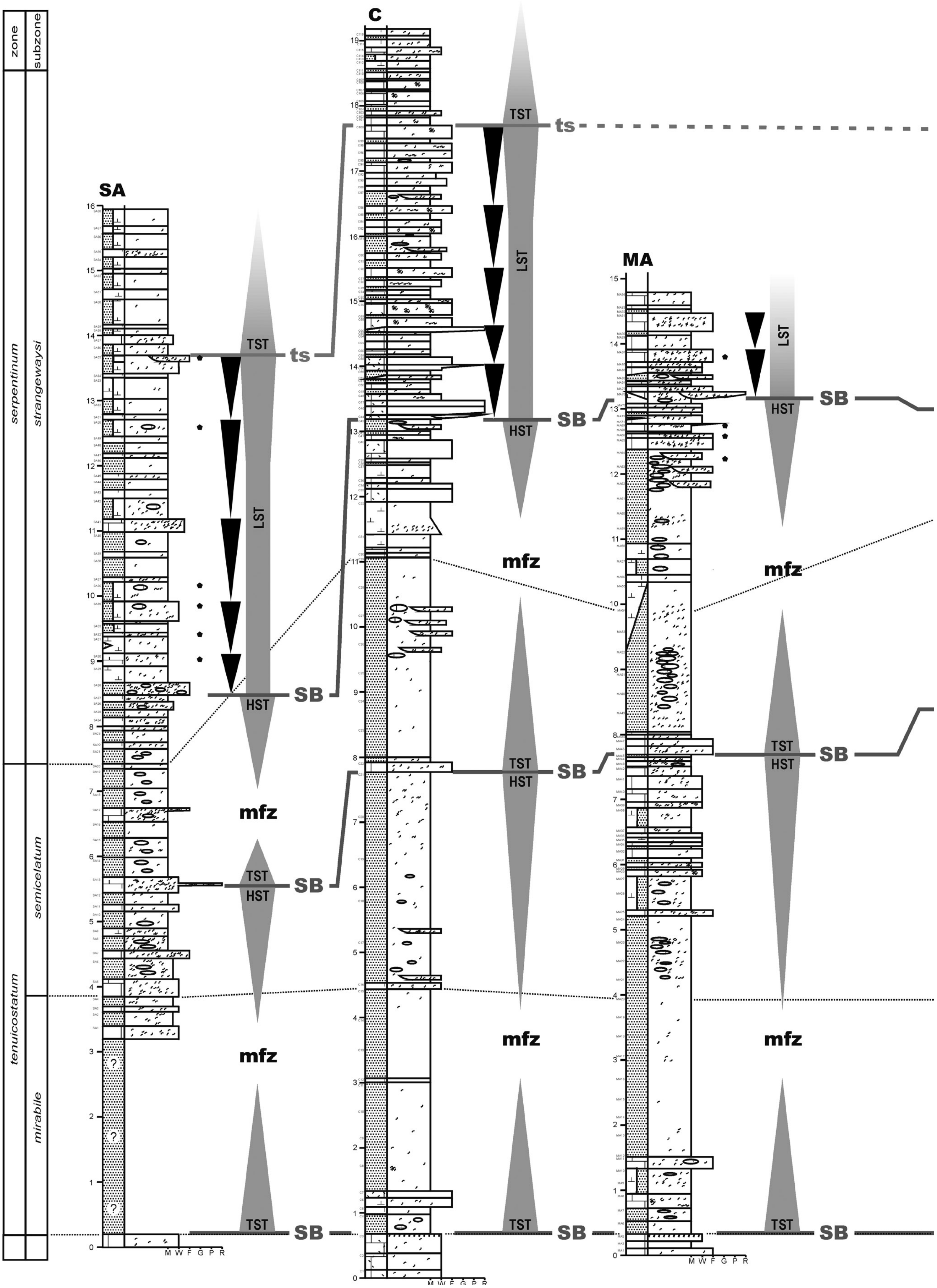
- *Katosira - subset*

Table 3.–Benthic faunal communities from the Lower Toarcian of the Iberian Peninsula, described in Gahr (2002). In some of the subsets, HD and LD are abbreviations for High Diverse and Low Diverse respectively.

Tabla 3.–Communidades macrobentónicas del Toarciense Inferior de la Península Ibérica, descritas en Gahr (2002). En unos de los *subsets*, HD y LD significan High Diverse y Low Diverse respectivamente.

In the La Almunia section (AL) the *Zeilleria cornuta*-assemblage is tied to sequence boundary Tc 2, and the *Sphaeroidothyris perfida*-subset and (in the section Barranco Santa María, SA) the *Sphaeroidothyris dubari* HD-subset are tied to the base of the transgressive systems tract of the depositional sequence Tc 3.

As shown above, the low sedimentation rates produce an increasingly firmer substrate, in which epifaunal suspension feeders and larger infaunal organisms dominate the highly time-averaged community relicts. As pointed out by Gahr (2002), bivalves dominate over brachiopods under normal environmental conditions at mid-shelf depths. The mentioned community relicts, however, are


zone
subzone
serpentinum
strangewaysi
tenuicostatum
semicelatum
mirabile
SA
C
MA
TST
LST
HST
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SB
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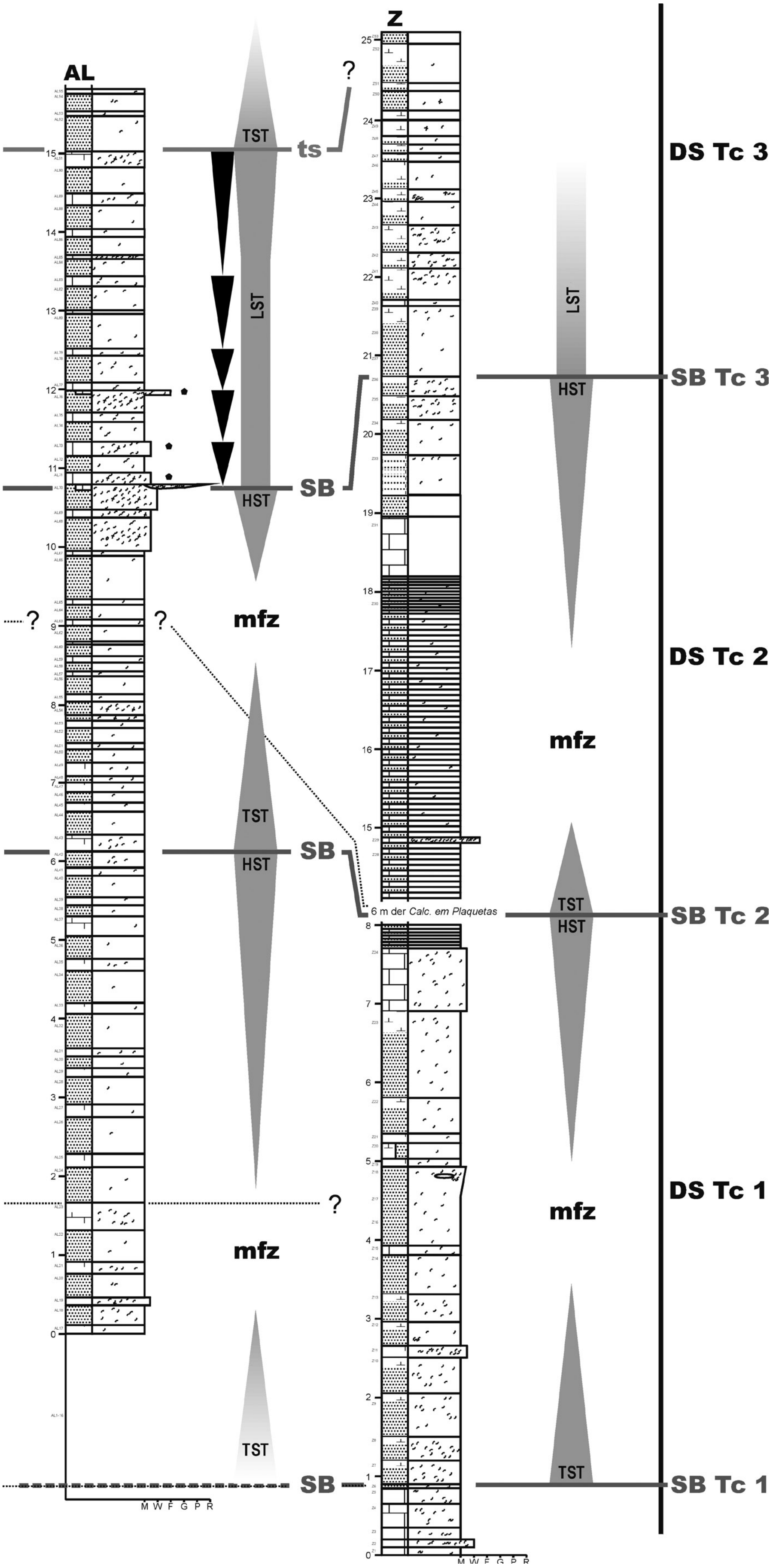

Fig. 6.–Sequence stratigraphic interpretation of the sections. For abbreviations see Table 2; parasequence sets in black; from Gahr (2002).

Fig. 6.–Interpretacion de la sequencia estratigráfica de las secciónes diferentes. Abreviaciones ve Table 2; parasequence sets en negro; tomada de Gahr (2002).

	Celtiberian Chains		Lusitanian Basin		Total	
Number of taxa	179		48		183	
Bivalves	115	64,2 %	23	47,9 %	116	63,4 %
Brachiopods	31	17,3 %	17	35,4 %	34	18,6 %
Gastropods	23	12,8 %	4	8,3 %	23	12,6 %
Serpulids	5	2,8 %	3	6,3 %	5	2,7 %
Corals	2	1,1 %	-	-	2	1,1 %
Decapods	1	0,6 %	-	-	1	0,5 %
Bryozoans	1	0,6 %	-	-	1	0,5 %
Echinoids	1	0,6 %	1	2,1 %	1	0,5 %
Epifaunal/semi-inf.	130	72,6 %	39	81,3 %	134	73,2 %
Infaunal	49	27,4 %	9	18,8 %	49	26,8 %
Filtrating	144	80,4 %	42	87,5 %	148	80,9 %
Herbivorous	21	11,7 %	4	8,3 %	21	11,5 %
Deposit-feeding	7	3,9 %	2	4,2 %	7	3,8 %
Carnivors	5	2,8 %	-	-	5	2,7 %
Microcarnivors	2	1,1 %	-	-	2	1,1 %

Fig. 7.–The composition of the benthic fauna in the Lower Toarcian of the Lusitanian Basin and the Celtiberian Chains; modified from Gahr (2002).

Fig. 7.–Composición de la fauna bentónica del Toarciense Inferior de la Cuenca Lusitánica y la Cordillera Ibérica; modificada de Gahr (2002).

clearly dominated by brachiopods (Gahr, 2002), indicating limitation by an environmental parameter other than substrate.

According to Steele-Petrović (1975; 1976; 1979), in the Mesozoic brachiopods dominate over bivalves only under two specific conditions:

(1) In contrast to the bivalves, the open constructions of the brachiopods lophophores prevent from clogging with sediment particles in a high-energy environment.

(2) As brachiopods are able to assimilate dissolved substances, they are not dependent on filtering food particles out of the water. This is an advantage during times of low influx of particulate food.

As in the present rock successions high-energy conditions can be ruled out, a low supply of particulate organic matter connected to lowered sedimentation rates is the most probable cause for the predominance of the brachiopods. This hypothesis is supported by the observations of Fürsich *et al.* (2001), who regard the considerably small size of the bivalves in the Lower Toarcian at a further locality in Spain as possible signs of stunting controlled by environmental factors. The scarcity of deposit-feeding taxa in the sections described here could be further evidence for the deficiency of nutrient particles (Gahr, 2002).

In the sections Barranco Santa María (SA), Barranco de la Cañada (C) and Barranco de la Masía (MA), the sequence boundary Tc 2 is not clearly developed. Therefore, and for faunal reasons, it is discussed within the chapter “Faunal community relicts of the middle to higher highstand systems tract” (see below).

3.2.2. Faunal community relicts of the low to middle transgressive systems tract

At the base of the transgressive systems tract, sedimentation rates are still low (see last chapter), slightly increasing towards the middle of the transgressive systems tract. At the low to middle transgressive systems tract of the depositional sequence Tc 1 and depositional sequence Tc 2, in two sections (Barranco de la Cañada, C, and Barranco de la Masía, MA) faunal associations occur, which are dominated by *Gryphaea* cf. *sublobata.* This epifaunal oyster has two different modes of life: cemented on large sediment particles such as bioclasts (which are very common in the sediments of the here described interval) or lithoclasts in the juvenile stage, and free-living (as a cup-shaped recliner) in the adult stage. With this life habit, the bivalve is well adapted to environments with generally low and only temporarily higher sedimentation rates.

In contrast to the brachiopod-dominated associations described above, brachiopods only play a minor role in associations dominated by *Gryphaea* cf. *sublobata*. As already mentioned, this could be due to a (slightly) increased influx of nutrient particles. As also the sedimentation rate increases, this appears to be very likely a second cause for the change of fauna.

3.2.3. Faunal community relicts of the higher transgressive systems tract

Towards the maximum flooding zone, sedimentation rates decrease again. Connected to that, also the supply of food particles decreases, favoring brachiopods, which are less dependent on this nutrient source (see above). As a result, the fauna of this interval is again dominated by brachiopods.

The following associations occur: *Lobothyris subpunctata*-subset (transgressive systems tract of the depositional sequence Tc 2 of the Barranco de Santa María section), *Lobothyris arcta* - *Liospiriferina undulata*-subset (transgressive systems tract of the depositional sequence Tc 2 in the Barranco de Santa María [SA], Barranco de la Cañada [C], and Barranco de la Masía [MA] sections), *Liospiriferina undulata*-subset (transgressive systems tract of the depositional sequence Tc 2 in the sections Barranco de la Cañada and Barranco de la Masía), and *Liospiriferina rostrata*-association (in the transgressive systems tract of depositional sequence Tc 1 and depositional sequence Tc 2 of the La Almunia section).

According to Fürsich and Hurst (1974), spiriferinid brachiopods such as *Liospiriferina* have the most efficient lophophores and thus are favored under the here described low energy/low food supply conditions.

During the Mesozoic, bivalves show a tendency to displace brachiopods from shallower marine habitats, which then moved to still deeper regions. Such a shift to deeper habitats with less biological stress might therefore be a further reason for the predominance of brachiopods in this interval of rising sea level.

3.2.4. The maximum flooding zone

With respect to the fauna, the most striking feature of this interval is the scarcity of the fauna, which can (apart from the maximum flooding zone of the depositional sequence Tc 1 of the Maria Parès section) be seen in the maximum flooding zone of the depositional sequence Tc 1 and the depositional sequence Tc 2 in all of the other sections.

Characteristic features of the maximum flooding zone are sediment starvation in combination with a low energy level (e.g. Emery and Myers, 1996). A certain amount of condensation can also be seen in the Barranco Santa María and the Barranco de la Cañada sections. However, as shown e.g. during times of the sequence boundary and the lowermost transgressive systems tract, these environmental factors do not exclude the settlement of a variety of organisms.

From contemporaneous sediments of other European regions (e.g. Great Britain, France and Germany), the development of black shales has been documented, indicating anoxic conditions at least at the sea floor (e.g. Jet Rock, schistes cartons, Posidonienschiefer). In the sections described here, no black shales were deposited. However, in the *tenuicostatum* Zone of these sections sediments are markedly darker in color, indicating a higher content of organic material and/or dispersed pyrite. Rare pyritized gastropods and ammonites and the presence of secondarily crystallized gypsum as a product of the weathering of pyrite document a primarily higher content of sulphur in the sediment, and thus low oxygen content, inimical conditions for most benthic faunal elements. The low energy conditions during the maximum flooding zone and a corresponding lack of circulation in the water column could have well contributed to this. The abundant presence of *Trichichnus* sp. as the only trace fossil in these layers supports this interpretation (McBride and Picard, 1991; Fürsich, 1998; Gahr, 2002), as does the composition of benthic ostracods in the Lower Toarcian of Spain (Whatley *et al.*, 1994).

Besides the documented primary absence of most benthic organisms due to at least temporary oxygen deficiency, a secondary disappearance of faunal elements due to early diagenetic shell dissolution cannot be ruled out. It is known that especially under euxinic conditions dissolved H_2S leads to a lowered pH value (e.g. Schmidt, 1991) and thus to increased dissolution of calcitic shells.

Further evidence for oxygen deficiency is given by the *Bositra buchi*-assemblage occurring in the *bifrons* Subzone (Middle Toarcian) of the Maria Parès section. However, due to the lack of comparable sections this bed cannot be placed into a sequence stratigraphic framework (Gahr, 2002). As at the present no similar beds are known from the Iberian Basin at this time, the oxygen deficiency most likely is a local event in the Lusitanian Basin.

3.2.5. Faunal community relicts in the lower highstand systems tract

A striking feature of the lower highstand systems tract in the Lower Toarcian of the Iberian Basin is the occurrence of the autochthonous *Corbulomima*-association which most likely can be correlated over several 10 km laterally (Gahr, 2002). It has been found in three sections: in the highstand systems tract of the depositional sequence Tc 2 of the Barranco Santa María section (SA) and highstand systems tract of the depositional sequence Tc 1 and in depositional sequence Tc 2 of the sections Barranco de la Cañada (C) and Barranco de la Masía (MA).

The change of the sea level trend from transgressive to regressive leads to higher sedimentation rates and an increased deposition of nutrient-rich terrigenous sediments. This results in a fine-grained and soft substrate. The color of these sediments is markedly lighter than the underlying deposits, indicating a well-oxygenated sediment and free water circulation.

The diverse association is dominated by small infaunal bivalves, accompanied by semi-infaunal mud-stickers and free-living recliners. Epifaunal elements, such as brachiopods, are rare. The low rate of encrustation documents continuous sedimentation at normal rates. Infaunal community relicts with a very similar composition were already described from the Oxfordian of England and Northern France (Fürsich, 1977) and from the Kimmeridgian of the Lusitanian Basin (Fürsich and Werner, 1986; Werner, 1986). These similarities (partly up to species level) can be explained by ecological substitution, during which successive organisms occupy the same ecological niche as earlier organisms with an equal mode of life (Fig. 8). Together with small infaunal bivalves (*Corbulomima*, *Nicaniella* [*Trautscholdia*], *Palaeoneilo*, *Protocardia*) thin-shelled oysters occur, which due to their free-living mode of life (at least at the adult stage), were well adapted to the soft substrate (*Gryphaea* cf. *sublobata* and *Nanogyra nana* respectively). Semi-infaunal bivalves such as *Inoperna* and *Pinna* complete this fauna.

Not just individual taxa were substituted by organisms with similar mode of life, but nearly all dominant macrobenthic taxa (Fig. 8). This fact is even more impressing taking into account that the very similar communities were separated by millions of years.

According to Emery and Myers (1996), during the highstand systems tract salinity values can be reduced and some authors (e.g. Riegel *et al.*, 1986; Prauss *et al.*, 1991; Hesselbo *et al.*, 2000) even describe phytoplankton indicative of lowered salinity values of surface waters of the upper *tenuicostatum* Zone (Gahr, 2002). However, this biostratigraphic age does not correspond to the interval of the highstand systems tract of the present paper,

	Gahr (2002)	**Fürsich (1977)**	**Fürsich and Werner (1986)**
Region	Celtiberic Chains (Spain)	England and N-France	Lusitanian Basin (Portugal)
Age	Toarcian	Oxfordian	Kimmeridgian
Faunal community	*Corbulomima* - association	*Corbulomima* - association	*Mesosacella dammarensis* - *Corbulomima suprajurensis* - association
Free-reclining oysters	*Gryphaea* cf. *sublobata*	*Nanogyra nana*	(*Exogyra* sp.)
Semi-infaunal mud-stickers	*Inoperna sowerbiana*, *Pinna* cf. *folium*	(*Pinna* sp.)	*Inoperna perplicata*
Small corbulids	*Corbulomima* cf. *obscura*	*Corbulomima* sp. A, *Corbulomima suprajurensis*	*Corbulomima suprajurensis*
Small astartids	*Nicaniella* cf. *voltzi*, *Nicaniella* sp. A	*Trautscholdia* (errore pro *Nicaniella*) *extensa*	*Nicaniella* sp. nov., *Nicaniella cingulata*
Small malletiids	*Palaeoneilo galatea*	*Mesosaccella* sp.	*Mesosaccella dammarensis*
Small protocardiids	(*Protocardia striatula*)	*Protocardia dyonisea*	*Protocardia peraltaensis*

Fig. 8.–Ecological substitution in *Corbulomima*-rich faunal communities. Taxa in hyphens do not occur in the trophic nucleus; modified after Gahr, 2002.

Fig. 8.–Substitución ecológica en comunidades abundantes en *Corbulomima*. Taxones en paréntesis no son parte del nucleo trófico; modificada de Gahr, 2002.

and even though the infaunal bivalve *Corbulomima* is known to tolerate such slightly reduced salinities (e.g. Fürsich and Werner, 1984), the accompanying fauna (also including some stenohaline brachiopods) does not indicate such lowered salinities (Gahr, 2000).

3.2.6. Faunal community relicts of the middle to higher highstand systems tract

As inferred from the faunal distribution, the higher sedimentation rates and the increased terrigenous influx only lasted a short time in the lower highstand systems tract, changing to slightly lowered sedimentation rates yet in the middle to higher highstand systems tract. In the highstand systems tract of the depositional sequence Tc 1 of the sections Barranco Santa María, Barranco de la Cañada and Barranco de la Masía, several faunal community relicts dominated by the two bivalves *Gryphaea* cf. *sublobata* and *Plicatula spinosa* occur, above all the *Gryphaea* cf. *sublobata* - HD-subset, *Gryphaea* cf. *sublobata* - LD-subset, and the *Plicatula spinosa* - *Dorsoserpula* sp. - subset.

As described above, *Gryphaea* cf. *sublobata* was epifaunal, cementing as a juvenile and free-living (as a cup-shaped recliner) in the adult stage. In contrast, *Plicatula spinosa* most likely was attached to a (in most cases secondary) hard substrate even as an adult organism (for a further discussion of this mode of life see Gahr, 2002).

Thus, *Gryphaea* cf. *sublobata* was also adapted to environments with at least temporarily higher sedimentation rates, whereas *Plicatula spinosa* and the often associated serpulid *Dorsoserpula* sp. depend on secondary hardgrounds which mainly result from concentration of bioclasts during times of low sedimentation rates. In the Barranco Santa María section and the Barranco de la Masía section the *Gryphaea* cf. *sublobata*-dominated associations alternate with those, which are dominated by *Plicatula spinosa*, thus most likely documenting changing sedimentation rates during the highstand systems tract.

The reason for the above mentioned only short time of normal deposition during the highstand systems tract might be the higher order transgressive trend throughout the Early Toarcian. This might also be the cause, why the sequence boundary Tc 2 is not markedly developed in the three sections. Therefore, even during this time, and, as documented above, during the following low to middle transgressive systems tract of the depositional sequence Tc 2, the *Gryphaea* cf. *sublobata*-dominated associations prevailed in the mentioned sections.

Another association occurring in the middle to higher highstand systems tract is the *Soaresirhynchia* - association, consisting of a HD- and a LD-subset. These, in most cases nearly monospecific layers of *Soaresirhynchia bouchardi* are documented in the depositional sequence Tc 2 of all sections described in this paper. As a pedicle-attached organism settling on mostly secondary hardgrounds, this brachiopod found appropriate conditions during times, in which low to moderate sedimentation rates resulted in a stable sediment with many bioclasts.

However, even though the described environment was favorable for the rhynchonellid, this does not explain the very low diversity in these layers (occasionally they are monospecific - one would expect a more diverse fauna, at least with respect to brachiopods), and the regional extent of these beds. They not only occur in both basins of the Iberian Peninsula, but also are known from France (Alméras and Fauré, 1990), Algeria (Alméras and Elmi, 1993) and Morocco (Rousselle, 1975; Alméras, 1993) during this time. Here, certainly an overprint connected to opportunistic behavior played an important role (see below).

3.2.7. Faunal community relicts of the lowstand systems tract

Apart from a few allochthonous tempestite layers at the base, the sea level and the environmental conditions during the aggradational phase of the lowstand systems tract of the depositional sequence Tc 3 probably were quite constant. However, the commonly changing faunal compositions of this interval do not show a distinct trend. These changes in composition may reflect minor environmental changes but, on the other hand, could also document (at least to a certain degree) increased biological stress after the Early Toarcian extinction event.

3.2.8. Faunal community relicts of the depositional sequence Tc 1 in the Lusitanian Basin

The transgressive systems tract, maximum flooding zone and highstand systems tract of the depositional sequence Tc 1 in the Maria Parès section (Z) show distinct faunal changes in the Lusitanian Basin. There, nearly throughout the whole depositional sequence Tc 1 two association subsets occur, namely the *Nannirhynchia* - *Plicatula spinosa*-subset and the *Plicatula spinosa* - *Liospiriferina villosa*-subset. In the lowermost transgressive systems tract and the maximum flooding zone the *Plicatula spinosa* - *Liospiriferina villosa*-subset occurs, while in the middle transgressive systems tract and the lowermost highstand systems tract the *Nannirhynchia* - *Plicatula spinosa*-subset dominates. With respect to the sedimentation rates (very low in the lowermost transgressive systems tract and the maximum flooding zone and

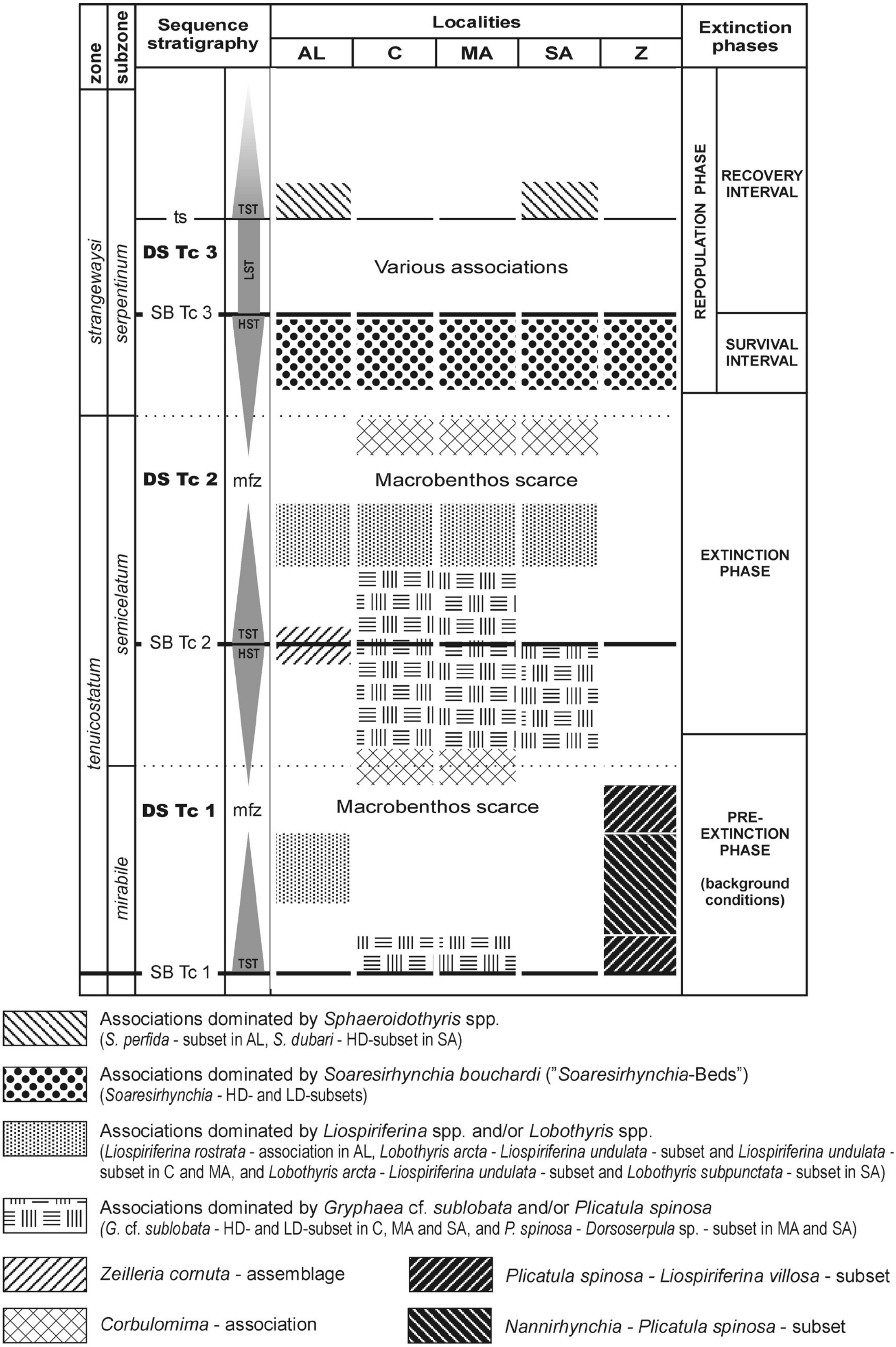

Fig. 9.–Stratigraphic distribution of macrobenthic associations in the Lower Toarcian at five localities of the Iberian Peninsula and their correlation with sequence stratigraphy and extinction phases.

Fig. 9.–Distribución estratigráfica de asociaciones macrobentónicas en el Toarciense Inferior de cinco localidades de la Península Ibérica y la corelación con sequencias estratigráficas y fases de la extinción en masa.

slightly higher in the middle transgressive systems tract and the lowermost highstand systems tract) this distribution agrees very well with the ecologic features of the associations as discussed in Gahr (2002).

The two tiny brachiopods (*Nannirhynchia pygmaea* and *Koninckella liasiana*), which are very common in the *Nannirhynchia* - *Plicatula spinosa*-subset, are only rarely found in the *Plicatula spinosa* - *Liospiriferina villosa*-subset. Together with this decrease, serpulids (in particular *Dorsoserpula* sp.) become abundant in the latter subset, pointing to a lowered sedimentation rate, which allowed the cementing organisms *Plicatula* and *Dorsoserpula* to settle on secondary hardgrounds such as shells and shell fragments. In contrast, the abundance of the tiny brachiopods may point to a slightly higher sedimentation rate. A temporarily lowered supply with food particles could also have favored the brachiopods, as they are not dependent on this source of food. However, one would expect lower supply with food particles to be connected with lower sedimentation rates - and this is not the case here. A competition for habitats as suggested e.g. by Aberhan (1993) might also be the cause for the differences in faunal composition.

3.3. Overprint during the Early Toarcian mass extinction event

As shown in Gahr (2001), the compilation of macrobenthic faunal lists of many publications documents an extinction event at the top of the *tenuicostatum* Zone. While many of the changes in faunal composition in the Upper Pliensbachian-Lower Toarcian interval can be explained by reactions to changes of environmental parameters (as shown above), these changes do not explain the sharp and distinct faunal change across the boundary between *tenuicostatum* and *serpentinum* Zone.

From a macrobenthic point of view, this change is documented by the disappearance of the long-term successful spiriferids (Alméras and Fauré, 1990; Vörös, 1993). Additional changes are found in the brachiopod fauna (like common zeilleriids and *Lobothyris* in the *tenuicostatum* Zone, but common *Homoeorhynchia* and *Telothyris* in the *serpentinum* Zone). In bivalves, common *Pseudolimea* and pectinid species were replaced by other limids and trigoniids, and cardiniid bivalves were heavily decimated (Palmer, 1975). At the same time, also microfossils show changes and even nektonic and planktonic organisms became affected (Gahr, 2001).

As pointed out earlier, the “pre-extinction phase” of the mass extinction events of Kauffman and Erwin (1995) the composition and distribution of the benthic fauna is clearly dependent on environmental parameters such as sedimentation rate, substrate, food supply and - to a questionable extent - oxygen availability and salinity. These factors prevailed also during the extinction phase in the higher *semicelatum* Subzone.

The middle to higher highstand systems tract of the depositional sequence Tc 2 coincides with the short survival interval of the repopulation phase, where, due to the prior extinction, only a low diversity benthic fauna existed. As a result, not only the appropriate substrate conditions for *Soaresirhynchia bouchardi*, but also the low numbers of competitive taxa, numerous free habitats and nutrient resources led to the opportunistic pattern of the rhynchonellid as a disaster taxon and the development of almost monospecific layers and the mentioned wide distribution of these layers at the base of the *strangewaysi* Subzone.

This hypothesis is supported by the abundance of a second opportunist in this interval (in the more distal Barranco Santa María section, SA), i.e. the infaunal brachiopod *Lingula* sp., which is known to have behaved as a disaster taxon also during the mass extinction at the Permian-Triassic boundary (Rodland and Bottjer, 2001).

The following recovery interval coincides with the aggradational phase of the depositional sequence Tc 3. As explained earlier, the frequently changing faunal compositions in this interval of quite constant environmental conditions do not show a distinct trend, but may reflect minor environmental changes.

However, at least to a certain extent, these changes very likely also document increased biological stress after the Lower Toarcian extinction event, due to the appearance of new species and/or genera as well as due to the reappearance of Lazarus-taxa (*sensu* Wignall and Benton, 1999), which have disappeared during times of the biological crisis.

4. Conclusions

It has been shown that in the Lower Toarcian of the Lusitanian Basin (Portugal) and the Celtiberian Chains (Spain), the composition and distribution of faunal community relicts follow distinct patterns (Fig. 9).

In both regions, occur at that time homoclinal carbonate ramp settings mostly below storm wave base with only a slight influence of siliciclastics. These sedimentary units can be interpreted in terms of sequence stratigraphy. In most cases, the boundaries of the sequence stratigraphic units can be determined by changes in faunal composition or Lithology. This is difficult for the end of the depositional sequence Tc 1 and the following sequence boundary Tc 1, indicating a transgressive trend that depresses the sequence boundary.

These units led to the identification of transgressive and regressive phases, which substantially influenced the environmental parameters at the sea floor, and thus also influenced the composition and the distribution of the benthic organisms. The recognized palaeoecological patterns correlate very well with the transgressive and regressive trends of the sea level, thus confirming this close connection.

In the case of the Lower Toarcian of the Lusitanian Basin and the Celtiberian Chains, there are main parameters, which controlled the composition and the distribution of the benthic fauna:

(1) Sedimentation rates control the grain size and stability of the substrate, especially the presence or absence of (mostly secondary) hardgrounds, such as bioclasts.

(2) The supply of particular organic matter (in most cases positively correlated with the sedimentation rate).

(3) To a lesser extent oxygen values (at least within the sediment) control the distribution of the benthic macrofauna.

(4) Although there are some hints that also lowered salinity values played a certain role in other regions, this cannot be confirmed here.

As these environmental parameters remained constant for a long geologic time, community relicts from different ages can be compared, an example being the *Corbulomima*-association.

However, besides the environmental parameters, which were controlled by the sea level changes, also biological factors influenced to the composition and distribution of the benthic fauna, especially during and after the Early Toarcian mass extinction event.

One of the most important biological parameters is the number of competitive taxa. If this number is low, as documented during the survival interval of the extinction event, opportunists can rapidly spread over a large area. If the number increases, as documented after the extinction event, increased biological stress can lead to unstable conditions and frequently changing faunal compositions. However, unlike in the case of opportunistic behavior, it is, unfortunately, in most cases hardly possible to directly prove the importance of these biological interactions.

In conclusion, in the Lusitanian Basin and the Celtiberian Chains the composition and distribution of the benthic fauna was controlled by environmental parameters only in the lowermost Toarcian (*tenuicostatum* Zone), whilst in the higher Toarcian (*serpentinum* Zone) biological parameters predominated.

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