

# Foraminiferal fauna recovered after the Late Permian extinctions in Iberia and the westernmost Tethys area

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## Abstract

The mass extinction at the end of the Permian has long been recognized as the greatest in the history of life. Foraminifers were common throughout the Permian–Triassic (P–T) interval and provide one of the best, and certainly the most informative, fossil records of the P–T crisis. This study addresses the recovery of foraminiferal faunas during the Triassic after the Late Permian extinction in the western Tethys, and particularly in Iberia, through the analysis of evolution rates both at the species and genus level. For the Tethys area in general, a rapid recovery of these faunas during the Olenekian is reflected by high rates of appearance of new taxa along with the reappearance of many “Lazarus” taxa. These taxa became stabilized throughout the Anisian and Ladinian, with a reduction in the rates of origination of new taxa and the presence of associations that were highly diversified, comprising large numbers of species.

The first foraminifers in the Triassic of Iberia can be observed at two different levels. The first of these is in the Upper Anisian, while the second level corresponds to the Upper Ladinian (Longobardian)–Lower Carnian. The Triassic associations of the basins of Iberia show paleobiogeographic characteristics that are generally “Tethyan”, most of these associations being well known for the “alpine” Triassic. For the Ladinian, some associations from NE Iberia (NE Iberian basin, Catalanian basin, and Pyrenean basin) also show “Germanic” affinities. Finally, also for the Ladinian, there is some evidence of the possible southward movement of faunas from the Sephardic domain to the Betic basin. This point, however, requires further investigation.

With the exception of faunas associated with the reefs of the Ladinian Catalanian basin, communities are usually of low diversity and typical of unstable, shallow marine facies.

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## 1. Introduction

The end of the Paleozoic saw one of the most significant events in the history of life on Earth; two

mass extinctions occurring within a period of some 8 My (Kaiho *et al.*, 2003) during the Late Guadalupian and Late Lopingian. Together these extinctions account for the disappearance of 75% to 96% of species, 83% of genera and 57% of the marine invertebrate families known to exist in the Permian (Sep-

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koski, 1989, 1990; Stanley, 1987; Erwin, 1993; Hallam and Wignall, 1997). These events led to the disappearance of the trilobites (although already in decline), the Rugosa and Tabulata corals, and notably

affected crinoids, brachiopods, bryozoans and ammonoids. The greatest losses were seemingly suffered by the shallow, warm water faunas of the Tethys (Stanley, 1987).

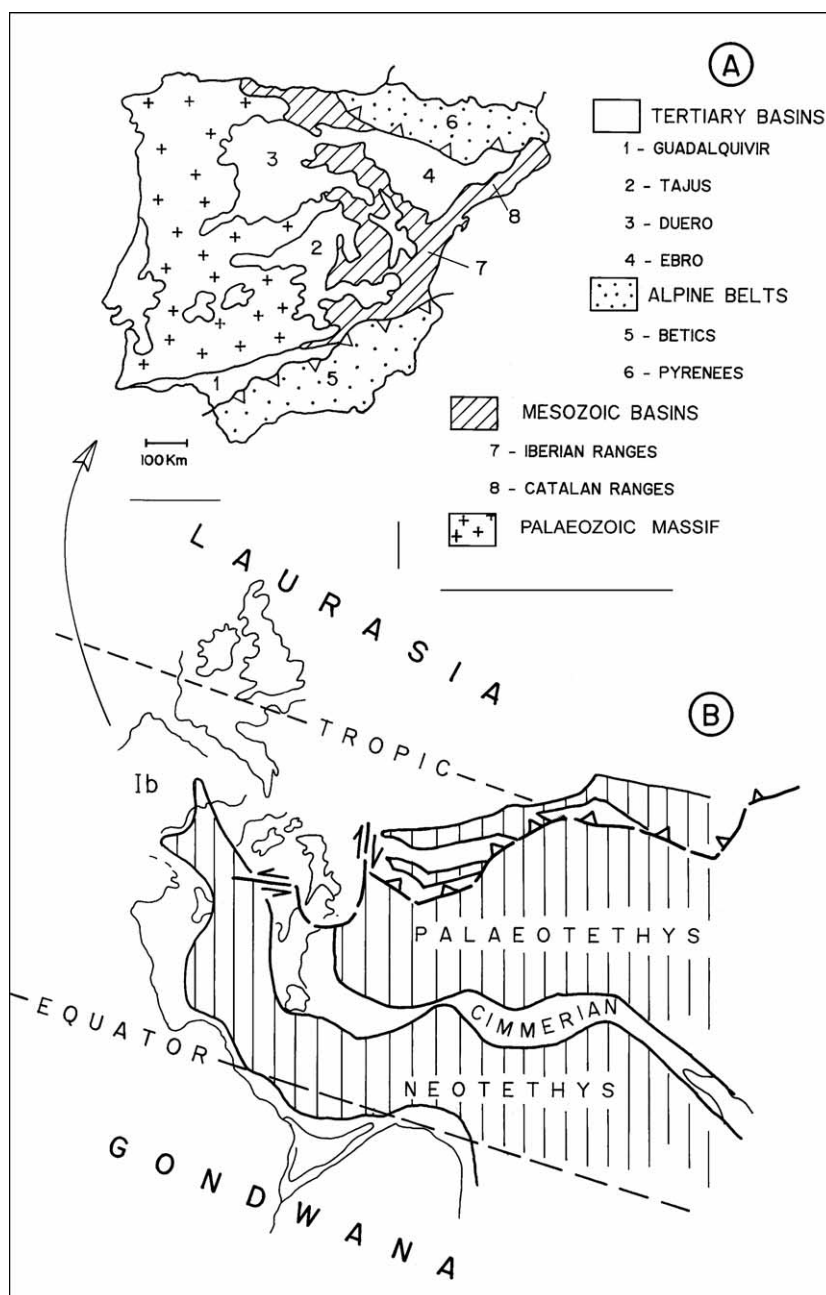


Fig. 1. (A) Geological sketch map of the Iberian Peninsula showing Mesozoic and Tertiary basins and main Alpine belts. (B) Paleogeographical reconstruction of western Tethys area for the Anisian. Ib—Iberia. Modified from Ziegler and Stampfli (2001).

If we look at the fates of Sepkoski's (1984) "evolutionary faunas", Cambrian fauna families diminished by 40%, Paleozoic families by 79%, and modern families by 27%. It should be noted, however, that the subsequent recovery of these faunas in the Triassic took place unevenly. Thus, modern faunas, which accounted for 40% of the Permian faunas, reached 70% of the diversity in the Middle Triassic, while the Paleozoic faunas underwent an additional mass extinction in the Late Triassic.

The marine biosphere at the start of the Triassic was therefore highly impoverished in taxa and there was an abundance of cosmopolitan elements and many empty ecological niches. Following this, during the first 10 My of the Triassic, radiation led to the appearance of several forms of ammonoids, bivalves, brachiopods, as well as the first forms of Scleractinia that were to construct the first reefs of the Middle Triassic (Ladinian).

Of the different suborders of foraminifera present in the Paleozoic: Allogromiina, Textulariina, Miliolina, Lagenina, Fusulinina and Involutinina, the number of families present in the Late Permian was reduced to half in the Early Triassic, while the number of genera fell by 75% (Tappan and Loeblich, 1988). Hence, the Late Permian saw the worst crisis in foraminifer history.

Extinction affected each group in a different way and was almost complete for the Fusulinina (although authors such as Loeblich and Tappan, 1987 consider that this suborder disappeared completely at the Permian–Triassic boundary), but had less of an impact on Textulariina (wiping out 30% of genera) and Miliolina (wiping out 50% of genera) (Tappan and Loeblich, 1988). Given the highly selective nature of foraminiferal extinction, we were able to evaluate which ecological-environmental traits were best suited to survival. As a general rule, extinction mostly affected the larger forms (Fusulinacea) living in shallower environments, along with forms of complex inner structure, irrespective of suborder (Brasier, 1988). All these forms are generally characteristic of tropical platforms. Less affected were smaller forms with less complex inner structures (microforaminifers) living in deeper zones and sometimes linked to dysaerobic facies (Tosk and Anderson, 1988). Tappan and Loeblich (1988) suggest that this relative survival could have something to do with the flattened, lenticular and

low trochoid tests of some these smaller species. Such morphologies are characteristic of infaunal detrital feeders and these therefore would not be susceptible to primary productivity crashes in the same way as other groups more dependent on the food chain (Tappan and Loeblich, 1988).

The present investigation examines the recovery and origination of foraminifer faunas during the Early and Middle Triassic after the Late Permian crisis in the western Tethys region, paying particular attention to their recovery in Iberia (Fig. 1). For an initial approach to this subject, the reader is referred to Plasencia et al. (2003).

The Tethys Sea reached Iberia for the first time during the Anisian. During latest Permian–Anisian times, an extensional tectonic regime prevailed across the eastern half of the Iberian Plate, leading to the development of the main Iberian Permian–Triassic basins (Fig. 1) (Ziegler, 1988; Stampfli and Borel, 2002) and to present-day ranges, formed through the Tertiary inversion of these basins (Salas and Casas, 1993; Arche and López-Gómez, 1996). The subsidence rate was moderate to low, and diminished with time in all the basins. Sedimentary infilling was very similar for all the basins (Buntsandstein facies), being mainly of alluvial origin. At the beginning of the Anisian, the Tethys sea successively prograded over the eastern margin of the plate during at least five major transgression–regression cycles, each one onlapping further westward with time (López-Gómez et al., 1998): the Röt-lower Muschelkalk (Anisian), middle-upper Muschelkalk (latest Anisian–Ladinian), lower Keuper (Carnal), upper Keuper (Late Carnian–Norian) and Imón or Isábena Formation carbonates (Late Norian). In the different Iberian basins, the Muschelkalk (divided into lower, middle and upper when well-developed) is represented by formal units for each basin. These units are described in detail in López-Gómez et al. (1998).

## 2. Materials and methods

Two methodological approaches were used. First, the recovery and evolution rates of the group under study were correlated both at the species and genus level. The evolution rates considered were: rate of origin of new taxa, rate of extinction, and net increase

rate. An ample discussion on the use of this method may be found in Márquez and Trifonova (2000). For calculations related to species (228), we used the data of Márquez and Trifonova, modified according to Menning's (1995) chronostratigraphic scale. For calculations on genera (121), information was used on the stratigraphic ranges reported by Sepkoski (2002), Loeblich and Tappan (1987), Trifonova (1992, 1993, 1994, and unpublished data), Salaj et al. (1983), Gaździcki (1983), Zaninetti (1976), Oravecz-Scheffer (1987) and Rettori (1995), among others. We selected genera for which stratigraphic ranges were well established. Tables 1 and 2 and Figs. 2 and 3 show the evolution rates calculated. Stratigraphic ranges for the different genera considered are provided in Table 3.

It should be mentioned that according to some authors the stratigraphic range for the suborder Fusulinina ends at the Permian–Triassic boundary (Loeblich and Tappan, 1987; Tappan and Loeblich, 1988; Sepkoski, 1992). However, in previous works (Loeblich and Tappan, 1964, 1984) these same authors locate the extinction of Fusulinina in the Upper Triassic. Notwithstanding, almost all experts in Triassic foraminifers (Zaninetti, 1976; Salaj et al., 1983; Oravecz-Scheffer, 1987; Trifonova, 1992, 1993, 1994; Rettori, 1995, and so on) consider that certain superfamilies of this suborder, such as Geinitzinacea, Endothyraea, Earlandiacea, Moravaminacea and Nodosinellacea, survived the extinction only to reappear in the Triassic with a large number of species, and several new genera and families from the Triassic have been described (Zaninetti et al., 1992; Vachard et al., 1994). Here, we follow this criterion and consider all these species as belonging to the suborder Fusulinina.

Table 1

Speciation rates, extinction rates, and net rates of increase obtained from Márquez and Trifonova (2000, modified)

Species			
Stages	Rate of origin of new taxa	Extinction rate	Net rate of increase
Rhaetian	0.01	0.18	−0.17
Norian	0.03	0.04	−0.02
Carnian	0.04	0.06	−0.02
Ladinian	0.14	0.06	0.09
Anisian	0.18	0.08	0.10
Olenekian	0.21	0.10	0.11
Induan	0.11	0.00	0.11

Table 2

Rates and origin of new genera, extinction rates, and net rates of increase obtained from data in Table 3

Genera			
Stages	Rate of origin of new taxa	Extinction rate	Net rate of increase
Rhaetian	0.02	0.11	−0.09
Norian	0.02	0.02	0.00
Carnian	0.03	0.02	0.01
Ladinian	0.04	0.02	0.02
Anisian	0.09	0.02	0.07
Olenekian	0.11	0.04	0.07
Induan	0.01	0.00	0.01

In the second part of this study, we recompiled the main references with descriptions of foraminifer associations found in the different regions of the western Tethys area for the Lower and Middle Triassic. For Iberia, this recompilation refers to a broader range, and faunas appearing in its different paleogeographic domains are indicated (Figs. 4 and 5).

### 3. Recovery of foraminifera in the western Tethys area

#### 3.1. Lower Triassic

The Lower Triassic Scythian shows two clear diversification stages which can be ascribed to the Induan and Olenekian.

##### 3.1.1. Induan

For the lowermost Triassic, the first records of foraminifers appear in the eastern Tethys area (China) and are dominated by opportunist, eurifacial forms giving rise to associations that are sometimes numerous but of low species diversity, since they are mostly comprised of arenaceous genera (Tong and Shi, 2000).

In the eastern Tethys area, the recovery process seems to be dominated by forms of the suborder Miliolina. Among the most common species are *Coronospira mahajeri* Brönninann, Zaninetti and Bozorgnia and *Rectocornospira kalhori* Brönninann, Zaninetti and Bozorgnia, identified in many areas of Europe and Asia (Rettori, 1995). Trifonova (1993 and unpublished data) found these species in the Lower Triassic (Dinerian-Smithian undivided) of Bulgaria, in

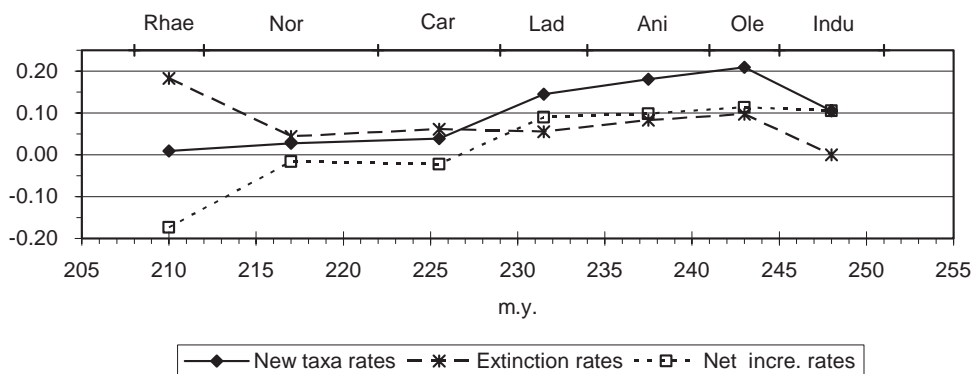


Fig. 2. Speciation rates, extinction rates and net rates of increase obtained from Table 1. Note maximum production of new species during the Olenekian (values higher than 0.2 nov sp./m.y.). These values decreased during the Middle and Late Triassic. Abbreviations: Rhae=Rhaetian, Nor=Norian, Car=Carnian; Lad=Ladinian, Ani=Anisian; Ole=Olenekian; Indu=Induan.

levels of the *Meandrosira cheni* Zone described by Salaj et al. (1988), along with species of the genus *Kamurana* (*K. bronnimanni* Altiner and Zaninetti and *K. chatalovi* Trifonova).

The genus *Meandrosira* is highly significant from the standpoint of the biostratigraphy of the Lower Triassic. Kristan-Tollmann (1984) described the first Triassic species of this genus, *Meandrosira dieneri* Kristan-Tollmann, at the base of the Griesbachian (Lower Induan) of the Kumaun region of the central Himalayas. Trifonova (1993 and unpublished data) also noted the presence of *M. dieneri* in levels of the Dinerian-Smithian (*M. cheni* Zone) of Bulgaria together with *M. cheni* Ho. Associated with these forms of *Meandrosira* and at the same levels in Bulgaria, Budurov and Trifonova (1991) identified

several species of *Hemigordius* (*H. cf. baoqingensis* Wang and *H. brunni* Lys) and *Hemigordiopsis* (*H. irregularis* Wang and Sun and *H. renzi* Reichel). This association is completed in the Lower Triassic of Bulgaria (Budurov and Trifonova, 1991) by several species such as *Glomospira sinensis* Ho, *Glomospira simplex* Ho and *Glomospirella shengi* Ho. A detailed review of these taxa allowed Rettori (1995) to consider them synonymous and ascribe them all to the species *Hoyenella sinensis* (Ho).

### 3.1.2. Olenekian

During the Olenekian, Triassic faunas in general started to quickly diversify. Foraminifers showed high rates of appearance of new taxa (Tables 1 and 2 and Figs. 2 and 3), as would be expected for a

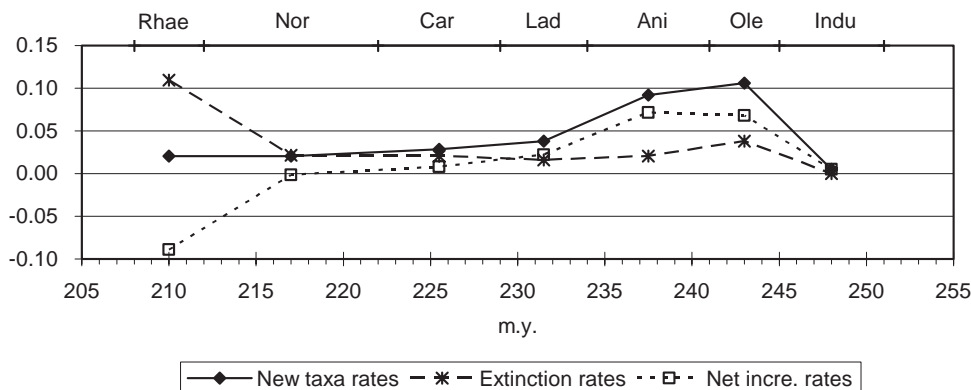


Fig. 3. Rates of origin of new genera, extinction rates and net rates of increase obtained from data in Table 2. As for species, the maximum production of new genera appeared during the Olenekian, diminished during the Anisian, and reached values close to zero in the Ladinian (see text). See Fig. 2 for abbreviations.



situation in which many ecological niches became available after the Late Permian extinctions. It should be noted that high extinction rates are recorded for both species and genera. These rates are the highest of the Triassic if we exclude the Rhaetian extinction (Tables 1 and 2). Similarly, we should also mention the reappearance of many taxa already present in the Permian among the faunas of the Olenekian (“Lazarus” taxa) (Table 3).

With regard to the recovery of foraminifer faunas in the western Tethys domain, the Upper Olenekian is characterised by the presence of the species *Meandrospira pusilla* (Ho), widely described by many other authors including Zaninetti (1976), Gaździcki et al. (1975), Salaj et al. (1983), Trifonova (1978, 1993), Rettori (1995), and so on. This species is particularly abundant in the lower part of the Spathian and characterises the *M. pusilla* Zone of Salaj et al. (1988).

Locally, the fauna related to the *M. pusilla* Zone can be relatively abundant, as indicated by Trifonova (1978 and unpublished data) and includes several species of the genera *Ammodiscus*, *Glomospira*, *Glomospirella*, *Hyppocrepina*, *Spiroplectammina*, *Bigennerina*, *Cornuspira*, *Nodogordiospira*, *Calcitornella*, *Earlandia*, *Fronndina*, *Nodosaria*, *Nodosinella*, and *Hoyenella*. In the northeastern region of Bulgaria (Trifonova, 1977a), an association appears in these levels in which, besides *M. pusilla*, we may also find isolated specimens of *Hyppocrepina dabravensis* Trifonova, *Cornuspira parapriscia* (Ho), *H. sinensis* (Ho), *Spiroplectammina dobrudzhiana* Trifonova, *Bigennerina vallis* Trifonova, *Nodogordiospira praeconversa* Trifonova, *Calcitornella perplexa* Trifonova, *C. mahajeri* Brönnimann, Zaninetti and Bozorgnia, *Glomospirella tenuifistula* Trifonova, along with several species of *Earlandia* such as *E. amplimuralis* (Pantić), *E. gracillius* (Pantić) and *E. tintinniformis* (Mišik).

In levels equivalent to the Upper Olenekian (Spathian), Rettori (1995) cites the presence of *M. cheni* (Ho), along with several *Arenovidalina* species such as *A. chialingchiangensis* Ho and *A. amyvoluta* Ho, described by Ho (1959) for China and cited for many European localities by Zaninetti (1976), Salaj et al. (1983) and Oravecz-Scheffer (1987).

The species *Pilamina praedensa* Urošević has been identified from the Spathian of East Serbia (Urošević, 1988) and the island of Hydra (Greece)

(Rettori, 1995), while the species *Gandinella silensis* (Dager) occurs on the Kocaeli Peninsula (Turkey) (Dager, 1978) and the Carpatians of Romania (Salaj et al., 1983).

Finally, other significant species appearing in the late part of the Early Triassic are *Krikoumbilica pelei-formis* He, which was initially described in the Middle Triassic of China but cited for the Spathian (Upper Olenekian) of the island of Hydra (Greece) (Rettori et al., 1994), *Endoteba controversa* Vachard and Razgallah, a species already occurring in the Permian and cited for the Early Triassic by Rettori (1995) and finally, *Triadodiscus eomesozoicus* (Oberhauser). The latter species begins the development of the Involutinacea, which eventually leads to their vast expansion during the Anisian and Ladinian.

### 3.2. Middle Triassic

#### 3.2.1. Anisian

The high rates of origination of new taxa (genera and species) for the Olenekian diminished during the Anisian and Ladinian, which, in turn, led to their stabilization as very low net increase rates (Tables 1 and 2; Figs. 2 and 3). The cause of this was the steady occupation of empty ecological niches since the Permian by new species, accompanied by the fact that marine environments became more stable throughout the Anisian and Ladinian. The end result is the appearance of much more stable and diverse living communities comprised of a large number of taxa. Thus, the number of genera present (confirmed plus inferred) in the Anisian (Table 3) is 69, while this number increases to 75 in the Ladinian. This clearly contrasts with the fauna of the Induan (33 genera) and Olenekian (47 genera). The numbers of species present (confirmed plus inferred, from Márquez and Trifonova, 2000) were 102 in the Anisian and 131 in the Ladinian. Once again these data contrast sharply with those for the Induan (31) and Olenekian (57). We should mention that, as occurred in the Olenekian, the Anisian saw the reappearance of several “Lazarus” taxa (see Table 3 for information on genera).

Extinction rates also approached values close to zero throughout the Middle and Late Triassic. However, this situation was to change radically in the Rhaetian with high rates of extinction recorded for

Table 3

Stratigraphical ranges for genera used in this paper

	Upper Permian	Triassic							Lower Jurassic
		Lower Triassic		Middle Triassic		Upper Triassic			
		Induan	Olenekian	Anisian	Ladinian	Carnian	Norian	Rhaetian	
<b>TEXTULARIINA</b>									
<i>Alpinophragmium</i>									
<i>Ammobaculites</i>	→								→
<i>Ammodiscus</i>	→	—	—	—	—	—	—	—	→
<i>Amnosiphonia</i>									
<i>Ammovevertella</i>	→								
<i>Bigenerina</i>			—						→
<i>Duotaxis</i>									
<i>Flagrospira</i>									
<i>Gandinella</i>			—	—	—	—	—	—	
<i>Gaudryina</i>				—	—	—	—	—	→
<i>Gaudrynella</i>				—	—	—	—	—	→
<i>Gaudrynopsis</i>						—	—	—	→
<i>Glomospira</i>	→	—	—	—	—	—	—	—	→
<i>Glomospirella</i>		—	—	—	—	—	—	—	→
<i>Hippocrepina</i>			—						→
<i>Hyperammina</i>	→								→
<i>Hyperamminoides</i>	→								→
<i>Kaeveria</i>									
<i>Labyrinthina</i>									→
<i>Lituotuba</i>									→
<i>Paleolituonella</i>									
<i>Paulbronnimannella</i>				—					
<i>Paulbronnimannia</i>				—	—				
<i>Pilamina</i>	→	—	—	—	—	—	—	—	
<i>Pilaminella</i>				—	—	—	—	—	
<i>Placopsilina</i>					—	—	—	—	→
<i>Plagioraphe</i>					—	—	—	—	
<i>Psammosphaera</i>	→			—	—	—	—	—	→
<i>Pseudobolivina</i>				—	—	—	—	—	→
<i>Rectoglomospira</i>			—	—	—				
<i>Reophax</i>	→				—	—	—	—	→
<i>Sorosphaera</i>	→			—	—				→
<i>Spiroplectammina</i>	→	—	—	—	—				→
<i>Tolypammina</i>	→		—	—	—	—	—	—	
<i>Trochammina</i>	→			—	—	—	—	—	→
<i>Verneuilinoides</i>			—	—	—	—	—	—	→
<b>FUSILININA</b>									
<i>Abriolina</i>				—	—	—	—	—	
<i>Caligella</i>	→			—	—	—	—	—	
<i>Earlandia</i>	→		—	—	—	—	—	—	
<i>Earlandinita</i>	→		—	—	—	—	—	—	
<i>Endoteba</i>	→	→	→	→	→	→	→	→	
<i>Endotebanella</i>			—	—	—	—	—	—	

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Table 3 (continued)

	Upper Permian	Triassic							Lower Jurassic
		Lower Triassic		Middle Triassic		Upper Triassic			
		Induan	Olenekian	Anisian	Ladinian	Carnian	Norian	Rhaetian	
<b>MILIOLINA</b>									
<i>Orthella</i>									
<i>Orthotrinacria</i>						---			
<i>Paraophthalmidium</i>									
<i>Paratriasina</i>									
<i>Planiiinvoluta</i>									
<i>Quinqueloculina</i>									
<i>Rectocornuspira</i>	---								
<i>Siculocosta</i>									
<i>Siphonofera</i>									
<i>Spiramphorella</i>									
<i>Turriplomina</i>									
<i>Urnulinella</i>						---			
<i>Vinelloidea</i>									
<b>LAGENINA</b>									
<i>Astaculus</i>									
<i>Austrocolomia</i>									
<i>Berthelinella</i>									
<i>Cryptoseptida</i>	→								
<i>Dentalina</i>									
<i>Eoguttulina</i>									
<i>Fronidina</i>	→								
<i>Glandulinoides</i>									
<i>Grillina</i>									
<i>Ichtyolaria</i>	→								
<i>Involutaria</i>									
<i>Lenticulina</i>									
<i>Lingulina</i>									
<i>Nodosaria</i>									
<i>Pseudonodosaria</i>									
<i>Robuloides</i>	→								
<i>Sagoplecta</i>									
<i>Vaginulinopsis</i>									
<b>ROBERTININA</b>									
<i>Duostomina</i>									
<i>Diploremmina</i>									
<i>Involvina</i>									
<i>Krikoumbilica</i>									
<i>Oberhauserella</i>									
<i>Schmidita</i>									
<i>Variostoma</i>									

Note the number of Paleozoic taxa that reappear during the Early and Middle Triassic ("Lazarus Taxa"). Symbols: (A) Left side of the table: solid arrows indicate genera recorded in the Late Permian. Dashed arrows correspond to genera inferred in the Late Permian. (B) Right side of the table: continuous arrows correspond to genera recorded in the Early Jurassic, discontinuous arrows to genera cited in later periods.

both genera and species (Márquez and Trifonova, 2000) (Tables 1 and 2; Figs. 2 and 3).

Several genera and species that emerged and/or developed during the Anisian and Ladinian gave rise to characteristic faunal associations that have enabled some authors to establish various biozones (Salaj et al., 1983; Trifonova, 1984; Salaj et al., 1988). Among the most notable forms of the Anisian are *Meandrospira dinarica* Kochansky-Devidé and Pantić, very common in the Carpathian-Balkan zone and in the Alps (Rettori, 1995), and *Pilamina densa* Pantić, found in abundance in the Pelsonian of the Alps (Zaninetti et al., 1972), Poland (Gaździcki et al., 1975) and Turkey (Zaninetti and Dager, 1978). Another frequently occurring species is *Paulbronnimannia judicarensis* (Premoli-Silva), widely described in many sites of the western Tethys (Rettori, 1995) for the Pelsonian.

The superfamily Involutinacea began development in the Anisian, and attained considerable importance as populations of *Triadodiscus mesozoicus* (Oberhauser), a species from the Olenekian, grew. In addition, the first forms of *Aulotortus* and *Lamelliconus* emerged, genera that were to develop substantially during the Ladinian and Carnian.

The genus *Turriglomina* also developed during the Anisian and gave rise to many species of stratigraphic significance, such as *T. conica* (He), *T. mesotriasica* (Koehn-Zaninetti) and *T. scandonei* (Zaninetti, Ciarpica, Martini, Salvini-Bonard and Rettori). The species *Paleolitonella meridionalis* (Luperto) is also widely cited for the Middle Triassic of several Tethyan localities, especially in the Ladinian (Trifonova, 1992). Other genera developing in the Anisian are *Endoteba*, *Endotebanella*, *Endotriada* and *Endotriadella*, the species *Endotriadella wirzi* (Koehn-Zaninetti) being very common in the western Tethys (Rettori, 1995).

The foraminiferal faunas of the Anisian are widely represented in Bulgaria (Trifonova, 1978), with associations belonging to the biozones of *Meandrospira deformata* (=the *Meandrospira insolita* Zone) and of *P. densa* (Salaj et al., 1988). Thus, Trifonova and Vaptsarova (1982) report the presence of two biofacies with different foraminifer associations. In the first biofacies from shallow environments with hypersaline, well-mixed waters, it is common to find species of Textulariina, such as *Glomospira tenuifistula* Ho, *Glomospirella triphonensis* Baud, Zaninetti and Brönnimann, *Gl. amplificata* Kristan-Tollmann, and

*Trochammina almtalensis* Koehn-Zaninetti. Further components of these associations are *H. sinensis* (Ho), *Gaudrina seducta* Trifonova, *Earlandia tintiniformis* (Mišik) and *M. dinarica* Kochansky-Devidé and Pantić. The second biofacies corresponds to platform environments with well-mixed waters of normal salinity, sometimes linked to reef areas (Trifonova and Vaptsarova, 1982). The associated fauna includes *Turriglomina mesotriasica* (Koehn-Zaninetti), *Endoteba badouxi* (Zaninetti and Brönnimann), *E. kueperi* (Oberhauser), *E. wirzi* (Koehn-Zaninetti) and several Duostominidae, including *Duostomina alta* Kristan-Tollmann, *D. magna* Trifonova and *Diplostromina astrofimbriata* Kristan-Tollmann. Also common in these associations is the presence of the alga *Baccanella floriformis* (Pantić) (Trifonova, 1977b).

### 3.2.2. Ladinian

During the Ladinian there was a clear stabilization of marine ecosystems accompanied by the development of wide carbonate platforms bearing highly diversified communities. This period saw the appearance of the first coral reefs formed by Scleractinia corals, calcareous algae and sponges. Among the most frequently found forms in these environments in the western Tethys are numerous representatives of the Involutinacea, such as *Lamelliconus* gr. *biconvexus-ventroplanus* (Oberhauser), *L. multispirus* (Oberhauser), *L. procerus* (Liebus), *L. cordevolicus* (Oberhauser), *Aulotortus praegaschei* (Koehn-Zaninetti), *A. sinuosus* Weynschenk and *A. pragsoides* (Oberhauser) (Trifonova, 1992, 1993, 1994; Salaj et al., 1983; Oravec-Scheffer, 1987). The species *Pilaminella gemerica* Salaj also appears in abundance in the Ladinian, characterising the *P. gemerica* Zone. This zone is characteristic of reef facies and dasycladacean platform carbonate sediments (Salaj et al., 1988).

On the other hand, a number of Anisian species reach their height of development in the Ladinian. This occurs in the case of, among many others, *Paleolitonella meridionalis* (Luperto), *T. mesotriasica* (Koehn-Zaninetti), *D. astrofimbriata* Kristan-Tollmann, *D. subangulata* Kristan-Tollmann, *D. alta* Kristan-Tollmann, *D. magna* Trifonova, and several species of *Trochammina*, such as *T. almtalensis* Koehn-Zaninetti, *T. alpina* Kristan-Tollmann, *T. balcanica* Trifonova and *T. jaunensis* Brönnimann and Page. Numerous

Endothyracea can also be included here, such as *E. wirzi* (Koehn-Zaninetti), *Endoteba kueperi* (Oberhauser) and *E. badouxi* (Zaninetti and Brönnimann). Also frequent in the Ladinian of Bulgaria are species such as *Plagioraphe tornata* Kristan-Tollmann and *Nodogordiospira conversa* Trifonova (Trifonova, 1978). Finally many species of the Oberhauserellidae developed during the Ladinian, including *Oberhauserella ladinica* (Oberhauser), *O. mesotriassica* (Oberhauser) and *Schmidita inflata* FUCHS (Trifonova, 1994).

#### 4. Recovery in Iberia

The Lower Triassic in the Iberian Peninsula commences with continental deposits (Buntsandstein facies) while the Middle Triassic is essentially characterised by marine carbonate deposits (Muschelkalk facies) showing associations of foraminifers, conodonts, bivalves and ammonoids. Four main basins developed during the Lower–Middle Triassic in the Iberian Peninsula: the Iberian basin (with two branches: SW Castilian and NE Aragonese), the Pyrenean-Cantabrian basin, the Catalanian basin and the Betic basin. The Balearic Islands show a Middle–Upper Triassic stratigraphy similar to the External Zone Triassic of the Betic domain (López-Gómez et al., 2002).

The following sections review references made to the foraminifer faunas that appear in the different paleogeographic units, as these faunas recover in the Iberian Peninsula.

##### 4.1. Anisian

###### 4.1.1. Iberian ranges

The first marine levels of the Spanish Triassic have been dated as Upper Anisian (Pelsonian–Illyrian). These levels contain an already highly diversified fauna, similar to that found today in other regions of the Tethys realm, as may be established when we compare the descriptions with those of the previous section. In general, these first foraminifer associations of the Spanish Triassic are linked to times of a maximum transgression (Márquez, 1994).

Hence in the paleogeographic domain of the Iberian basin (Castilian branch) we find in the Dolomías de Landete Formation (lower Muschelkalk), a fauna comprised of diverse species such as *G. simplex*

Harlton, *H. sinensis* (Ho), *Glomospirella* cf. *triphonensis* Baud, Zaninetti and Brönnimann, *E. kueperi* (Oberhauser), *Meandrosira* cf. *dinarica* Kochansky-Devidé and Pantić and *P. judicarensis* (Premoli-Silva) (Márquez et al., 1994). This alpine-type association is considered part of the *P. densa* Zone of the biozones established by Salaj et al. (1988) for the Carpathian-Balkan domain, that is, Middle–Upper Anisian (Pelsonian–Illyrian). These faunas are characteristic of protected lagoon settings, with sporadic stages of agitation that coincide with the time of maximum transgression (Fig. 4).

Also for the Castilian branch, Pérez-Arlucea and Trifonova (1993) describe an association in the lower Muschelkalk (Albarracín Formation) composed of *P. judicarensis* (Premoli-Silva), *H. sinensis* (Ho), *Arenovidalina chialingchiangensis* Ho, *A. amyvoluta* Ho, *Pilaminella semiplana* (Kochansky-Devidé and Pantić) and several duostominids such as *D. astrofimbriata* Kristan-Tollmann, *D. subangulata* Kristan-Tollmann, *D. alta* Kristan-Tollmann and *D. magna* Trifonova. This association led these authors to date these levels as Pelsonian (upper Anisian).

###### 4.1.2. Catalanian ranges

In the Catalanian Ranges (Fig. 4), several species from the lower Muschelkalk have been described. Among these we find *H. sinensis* (Ho), *T. almtalensis* Koehn-Zaninetti, *E. tintinniformis* Mišik, *A. chialingchiangensis* Ho, *D. astrofimbriata* Kristan-Tollmann, *Calcitornella* sp., *Dentalina* sp. and *Nodosaria* sp. This association is characteristic of the top part of the *Pilamina densa* Zone of the Upper Anisian (Upper Pelsonian–Illyrian) (Budurov et al., 1993).

###### 4.1.3. Pyrenean Range

The presence of Anisian materials in the Pyrenean Triassic (Fig. 4) is indicated by the presence of *M. pusilla* (Ho) and *M. dinarica* Kochansky-Devidé and Pantić (Frechengues and Peybernes, 1991) on the southern side of the Pyrenean Range.

##### 4.2. Ladinian

###### 4.2.1. Iberian Ranges

In the upper carbonate section of the Muschelkalk, in the Castilian branch of the Iberian Ranges (Fig. 5), García-Gil (1990) identified forms attributed to *Mean-*

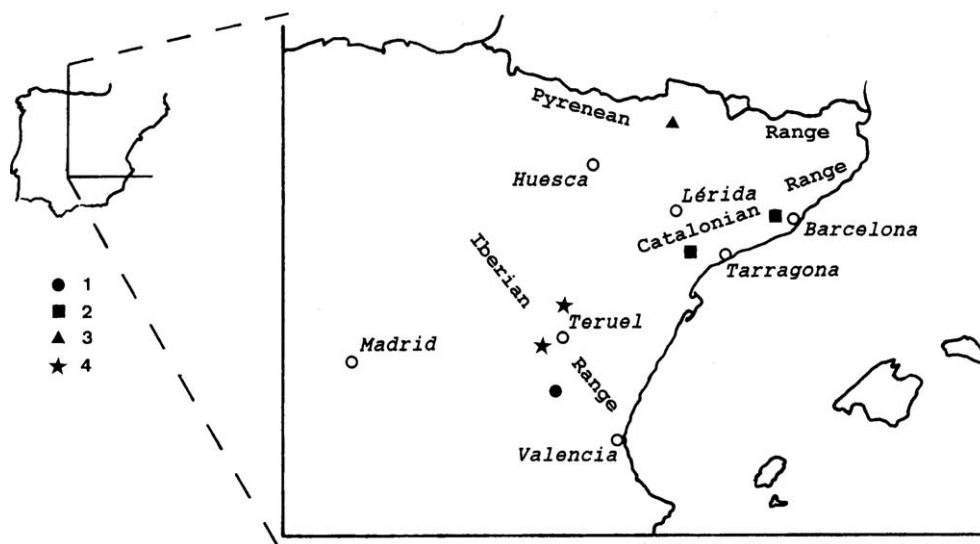


Fig. 4. Sites of the main localities for Anisian foraminiferal assemblages. 1—Márquez et al. (1994), 2—Budorov et al. (1993), 3—Frechengués and Peybernes (1991), 4—Pérez-Arlucea and Trifonova (1993).

*drospiranella* cf. *samuelyi* Salaj, *Glomospira* sp., *Glomospirella* sp. along with a few *Nodosariidae*. In adjacent areas, Pérez-Arlucea (1985) mentions the species *C. parapriscia* (Ho), *H. sinensis* (Ho) and *Glomospirella minima* Michalík, Jendrejáková and Borza, among others.

Pérez-Arlucea and Trifonova (1993) also report two foraminifer associations of Ladinian age. The first of these appears in the Tramacastilla Formation and is characterised by the presence of the *Involutinina*: *Lamelliconus biconvexus* (Oberhauser), *L. ventroplanus* (Oberhauser), along with *Ophthalmidium* cf. *fusiforme* (Trifonova) and *Nodosaria ordinata* Trifonova. This fauna indicates an age of Late Ladinian (Longobardian). The second association also belongs to the upper Muschelkalk (Royuela Formation) and is formed by *G. simplex* Harlton, *H. sinensis* (Ho), *G. shengi* Ho, *T. eomesozoicus* (Oberhauser), *N. ordinata* Trifonova and *Variostoma helictum* Tappan, faunal elements characteristic of the Late Ladinian–Carnian (Pérez-Arlucea and Trifonova, op. cit.).

In the Aragonese branch of the Iberian Ranges, and more specifically in the Calanda section (Fig. 5), foraminifers are represented by numerous *Nodosariidae*, such as *N. ordinata* Trifonova, *Nodosaria* spp., *Dentalina terquemi* DOrbigny, *D. subsiliqua* Franke, *D. hoi* Trifonova, *D. cf. gerkei* Styk, *D. zlabachensis* Kristan-Tollmann, *D. cf. bicornis* (Terquem),

*Astacolus* cf. *karnica* (Oberhauser) and *Pseudonodosaria polyarthra* (Kristan-Tollmann), as well as several species of *Miliolina* (*C. parapriscia* (Ho) and *H. sinensis* (Ho)), *Trochamminidae* (*T. almtalensis* Koehn-Zaninetti) and *Spirillinidae* (*Spirillina oberhauseri* Styk). These associations may be paleoecologically interpreted as occurring in shallow, low energy environments, with perhaps higher than normal salinity (Márquez-Aliaga et al., 1987, 1994). Two levels frequently show some *Involutinidae* as *T. eomesozoicus* (Oberhauser), *Aulotortus planidiscoides* (Oberhauser) and *Aulotortus praegaschei* (Koehn-Zaninetti). These faunas suggest greater marine influence which, although protected (i.e., bahia or lagoon) were probably related to periods of maximum advance of the sea during the transgression of the late Muschelkalk.

From the perspective of paleobiogeography, we should mention the frequent appearance in the Germanic area of forms such as *D. gerkei* and *S. oberhauseri*, along with involutinids, which are common in the alpine domain. The fact that the latter appear in the Muschelkalk of the Iberian Ranges supports the idea of Budorov et al. (1993) related to the possibility of correlating the Spanish Middle Triassic in Germanic facies with regions of the alpine basins. These involutinid associations may be assigned to the *T. mesotriasica* Zone (*A. praegaschei* Subzone) suggest-

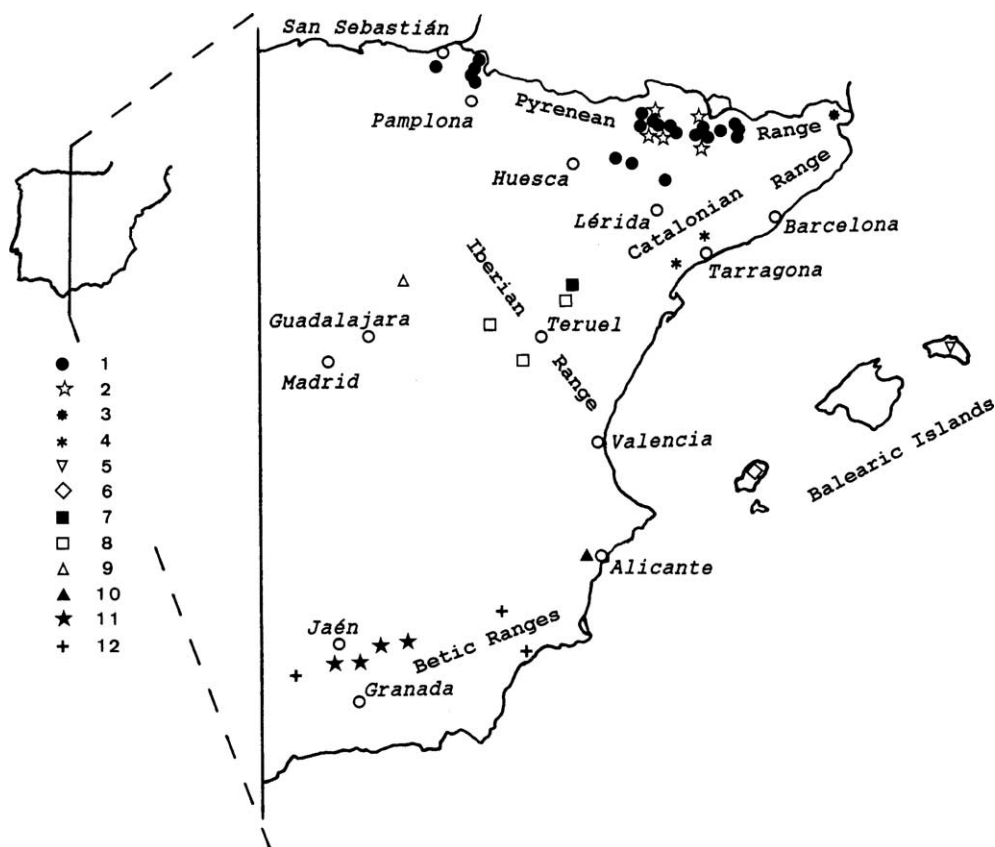


Fig. 5. Sites of the main localities for Upper Ladinian (Longobardian) foraminiferal assemblages. 1: Calvet et al. (1994a), Calvet et al. (1994b), Márquez et al. (1992). 2: Frechengues and Peybernes (1991). 3: Frechengues et al. (1990). 4: Márquez et al. (1989), Márquez et al. (1990), Márquez and Trifonova (1990), Márquez et al. (1991). 5: Vachard et al. (1989). 6: Rangheard and Colom (1967). 7: Márquez-Aliaga et al. (1987), Márquez-Aliaga et al. (1994). 8: Pérez-Arlucea (1985), Pérez-Arlucea and Trifonova (1993). 9: García-Gil (1990). 10: Márquez-Aliaga et al. (1993), López-Gómez et al. (1994). 11: Pérez-López (1991), Márquez and Pérez-López (2001). 12: Márquez et al. (2000), Pérez-López et al. (2003a,b).

ing a Late Ladinian (Longobardian) age (Salaj et al., 1988).

#### 4.2.2. Catalanian Ranges

The upper carbonate section of the Muschelkalk in the Catalanian Ranges (Fig. 5) has been the subject of several studies (Márquez et al., 1989, 1990, 1991; Márquez and Trifonova, 1990).

The first association of interest appears in the Rasquera Unit of the Dominio Baix Ebre-Priorat. Its fauna is a relatively rich and varied one from proximal deep ramp shallow environments (Márquez et al., 1991). The most outstanding species present are *Reophax asperus* Cushman and Waters, *Textularia* cf. *exigua* (Schwager), *E. tintinniformis* (Mišik), *Cyclogyra*

*pachygyra* (Güembel), *Calcitornella* sp., *Planinivoluta carinata* Leischner, *Agathammina* sp., *Ophthalmidium* sp., *Austrocolomia* cf. *marshalli* Oberhauser, *Grillina* aff. *oberhauseri* Sellier De Civrieux et Des-sauvage, *Nodosaria* spp., *Dentalina* cf. *cassiana* Güembel L, *Dentalina gerkei* Styk, *Duostomina* cf. *alta* Kristan-Tollmann and *Oberhauserella mesotriassica* (Oberhauser). These species again suggest the substantial influence of the Tethys since they are well known in the alpine basins of other zones of Europe and Asia, although some species, for example *D. gerkei*, are also found in Germanic facies. This foraminifer association indicates an age of Late Ladinian.

Communities of benthic foraminifers, much richer and more varied than previously, appear linked to the



reef complex of the Sierra de Prades (Tarragona province) (Márquez et al., 1990). The reefs have several facies: core, framework, flank and interreef facies, each showing different foraminifer associations.

The following taxa, among others, appear in reef core facies: *T. mesotriasica* (Koehn-Zaninetti), *R. asperus* Cushman and Waters, *T. almtalensis* Koehn-Zaninetti, *Agathammina austroalpina* Kristan-Tollmann and Tollmann and *D. alta* Kristan-Tollmann. In the reef framework it is common to find adhered forms (*Tolypammina gregaria* Wendt) and sandy forms such as *P. meridionalis* (Luperto), Earlandiidae (*Earlandia gracillis* (Pantić)), Duostominidae (*D. alta* Kristan-Tollmann), *Ophthalmidium exiguum* Koehn-Zaninetti and *O. mesotriasica* (Oberhauser).

In the upper part, reef complexes show a more varied fauna including *T. mesotriasica* (Koehn-Zaninetti), *P. tornata* Kristan-Tollmann, *T. almtalensis* Koehn-Zaninetti, *P. meridionalis* (Luperto), *E. wirzi* (Koehn-Zaninetti), *Lamelliconus multispinus* (Oberhauser), *Agathammina iranica* Zaninetti, Brönnimann, Bozorgnia and Huber, *O. exiguum* Koehn-Zaninetti, *D. alta* Kristan-Tollmann and *D. astrofimbriata* Fuchs. Many of these species normally occur in the alpine basins, as was noted above. The age indicated for these reef systems by foraminiferal associations is Late Ladinian (Longobardian) (Márquez et al., 1990).

#### 4.2.3. Pyrenean Range

In the Pyrenean Range, the carbonate upper Muschelkalk (Fig. 5) appears in several localities with different foraminifer associations. Of these, the most interesting is the association dominated by Involutinina that is linked to the Grey Limestone Unit (Calvet et al., 1994a,b). This association is related to periods of maximum flooding surface during the transgression of the late Muschelkalk (Márquez et al., 1992). Among the species present, we find *A. planidiscoides* (Oberhauser), *A. praegaschei* (Koehn-Zaninetti), *A. pragsoides* (Oberhauser), *L. multispinus* (Oberhauser), *L. procerus* (Liebus), *T. eomesozoicus* (Oberhauser), *S. oberhauseri* Styk, *Nodosaria* cf. *ordinata* Trifonova, *N. cf. zlambachensis* Kristan-Tollmann and *O. mesotriasica* (Oberhauser). These forms are typical of alpine areas, indicating a clear influence on the part of the Tethys. This level appears at several sites in the Pyrenean basin although it is best represented in the central-eastern region of the

range (in the Les Noguères-Cadí area). Its age can be ascribed to the Late Ladinian (Longobardian).

#### 4.2.4. Betic Ranges

Several foraminifer faunas have also been identified in the Betic Ranges. We should first mention the appearance of a poorly preserved, somewhat depauperate association in the upper Muschelkalk (Fig. 5) of Espejeras (Alicante province) (Márquez-Aliaga et al., 1993; López-Gómez et al., 1994). The species *Arenovidalina chialingchiangense* Ho has been identified alongside suspect *Aulotortus* and some *Nodosariidae*. The association indicates a probable Ladinian age.

The fauna of the Muschelkalk of the Betic Ranges Central Sector is much more complete and better preserved (Pérez-López, 1991) (Fig. 5). The association is one of shallow ramp settings and contains multiple species of Involutinina. Among these are *L. biconvexus* (Oberhauser), *L. procerus* (Liebus), *L. multispinus* (Oberhauser), *T. eomesozoicus* (Oberhauser), *L. cf. crassus* (Kristan), *L. cf. cordevolicus* (Oberhauser), *N. ordinata* Trifonova, *T. almtalensis* Kohen-Zaninetti, *P. carinata* Leischner, *O. exiguum* Kohen-Zaninetti and *D. alta* Kristan-Tollmann. This association is typically alpine and points to a Late Ladinian age (Longobardian).

In the Subbetic Zone of the Betic Ranges, the upper Muschelkalk (Márquez and Pérez-López, 2001) includes several foraminiferal assemblages in carbonate platform sediments. These are comprised of many species of Involutinina, such as *L. biconvexus* (Oberhauser), *L. procerus* (Liebus), *L. multispinus* (Oberhauser), *T. eomesozoicus* (Oberhauser), *A. planidiscoides* (Oberhauser), *A. praegaschei* (Koehn-Zaninetti), *A. pragsoides* (Oberhauser), along with species such as *P. gemerica* Salaj, *E. wirzi* (Koehn-Zaninetti), *O. mesotriasica* (Oberhauser), *D. alta* Kristan-Tollmann and *O. mesotriasica* (Oberhauser). According to the classic literature for alpine zones (Zaninetti, 1976; Salaj et al., 1983; Trifonova, 1992, 1993, 1994, and others), this association would appear to suggest a Late Ladinian (Longobardian)–Early Carnian age. However, preliminary data derived from other faunas (conodonts and ammonoids) found in the lower of these levels seem to point to an age earlier than the Longobardian. Moreover, Benjamini (1988) described a similar association in the Makhlesh Ramon series (Israel), with underlying levels ascribed



to the Uppermost Fassanian based on ammonoid fossils. In paleobiogeographic terms, these data would seem to indicate the arrival in southern Iberia of species from the Sephardic domain during the Early Ladinian (Fassanian), species that were to become common in alpine basins during the Late Ladinian (Longobardian).

The Triassic of the Internal Zones of the Betic Ranges (Malaguide Complex) also shows carbonate platform facies with an abundant macrofauna (Pérez-López et al., 2003b), along with conodonts (*Sephardiella mungoensis* (Diebel) and foraminifers (*O. mesotriasica* (Oberhauser). This fauna suggests a Ladinian age (Márquez et al., 2000).

Finally, we should indicate that in Muschelkalk carbonate facies of the External Zones of the Betic Ranges an assemblage of involutinids appears in several sections (*Lamelliconus* gr. *biconvexus-ventroplanus* (Oberhauser), *L. cordevolicus* (Oberhauser) and *T. eomesozoicus* (Oberhauser)). This association seems to coincide with the maximum flooding surface of a transgressive sequence and is ascribed to the Ladinian (Pérez-López et al., 2003a).

#### 4.2.5. Balearic Islands

The carbonate levels of the upper Muschelkalk in the Balearic Islands also contain foraminifera. On the island of Ibiza (Fig. 5), Rangheard and Colom (1967) mentioned and described numerous specimens of Nodosariidae species such as *Nodosaria raibliana* Gümbel, *N. sp.*, *Dentalina* sp. as well as specimens ascribed to *Lingulina* cf. *krebelsbergi* Oberhauser.

Foraminifers have also been identified in Middle Triassic levels in Menorca (Fig. 5). Among others, these include species of Involutinina (*Lamelliconus procerus* (Liebus), *T. eomesozoicus* (Oberhauser) and *Aulartortus praegaschei* Koehn-Zaninetti), indicating a Late Ladinian age (Vachard et al., 1989).

## 5. Discussion

### 5.1. Recovery of foraminiferal faunas in the western Tethys and Iberia

In general, during the Early Triassic (Induan and Olenekian), the recovery of foraminifer communities in the western Tethyan area was dominated by faunas

of the suborder Miliolina, while in the eastern area of the Tethys, faunas were mainly comprised of arenaceous genera. The most common species are those of the genera *Cornuspira*, *Hemigordius*, *Hemigordiopsis*, *Hoyenella*, *Kamurana*, *Meandrospira* and *Rectocornuspira* (suborder Miliolina) along with the genera *Ammodiscus*, *Glomospira*, *Glomospirella* and *Pilamina* (suborder Textulariina). Also present are some new forms of Fusulinina (*Earlandinita* and *Endotabanella*) and Involutinina (*Triadodiscus*). Associations generally exhibit high abundance although species diversity is low. Most of the components are cosmopolitan, opportunist and eurifacial species.

Given that the Lower Triassic of the Iberian Peninsula commences with continental deposits (Buntsandstein facies), the first marine foraminiferal faunas of Iberia are found in the Anisian. Thus, marine ecosystems had already recovered during the Early Triassic, such that the first Triassic foraminifers appearing in Spain are highly diversified and are similar to those appearing at that time in other zones of the Tethys realm, as indicated earlier in this article. In general, these first associations of the Spanish Triassic seem to be related to periods in which the flooding surface was at its maximum (Márquez, 1994), during which marine influence was greater, given the shallow depth of most Spanish basins.

So far, for the Middle Triassic of Spain, faunas from two of the biozones described by Salaj et al. (1988) have been identified. These faunas are related to the two carbonate sequences of the Middle Triassic in Germanic facies across most of Spain. Thus, for the lower Muschelkalk in the Iberian Ranges and Catalan Ranges, associations characteristic of the *P. densa* Zone have been identified, indicating a Middle–Late Anisian (Pelsonian–Illyrian) age. In the upper Muschelkalk, the foraminiferal fauna is comprised of species of the *T. mesotriasica* Zone (*A. praegaschei* Subzone), which would indicate a Late Ladinian age (Longobardian). Associations of this age have been observed in the Iberian Ranges, Pyrenean Range, Catalan Ranges, Betic Ranges and Balearic Islands (Ibiza and Menorca).

### 5.2. Evolution rates

The rate of appearance of new taxa notably increases during the Early Triassic, reaching its peak

in the Olenekian at 0.21 new species/My (Table 1) and 0.11 new genera/My (Table 2). During the Middle Triassic, rates decrease slightly, such that values for the Anisian are 0.18 new species/My and 0.09 new genera/My (Tables 1 and 2). Finally, in the Late Triassic, rates fall to values close to zero. As shown in Tables 1 and 2, net increase rates showed similar behaviour.

The pattern shown by these origination rates reflects a situation in which, following a mass extinction, many ecological niches became available, so that surviving faunas were able to rapidly diversify giving rise to new taxa and a net increase in rates. However, our data indicate a slight delay in the recovery of faunas, since peak appearance of new taxa rates correspond to the Olenekian, several million years after the Permian–Triassic boundary. Kozur (1998) attributes this delay to the development of dysaerobic conditions in shallow waters above storm-waves across vast areas of the Tethys during the Early Triassic (Induan). In the same way, Krull et al. (2004) propose that methane eruptions may have caused long-term adverse ecological conditions during the Early Triassic, preventing a swift ecological recovery. Hence, as the empty ecological niches steadily filled and marine ecosystems stabilized throughout the Olenekian and Middle Triassic, evolution rates decrease to values close to zero during the Late Triassic (Tables 1 and 2). The result is the emergence of ever more stable and diverse communities, including, by the Middle and Late Triassic, a large number of taxa.

If we compare evolution rates between the Triassic foraminifers (Tables 1 and 2; Figs. 1 and 2) and other groups at various times of diversification during the history of life, the diversification shown by foraminifers in the Early and Middle Triassic can be described as relatively moderate. The new taxa rate provided for bivalves in the Tertiary (Stanley, 1977) was 0.17 new species/My and the net increase rate is 0.063 species/My. Rates for mammals were much higher (Stanley, 1977): 0.89 new species/My and 0.22 species/My respectively. Similar calculations for the planktonic foraminifera of the Cenozoic (Berggren, 1969) yield rates ranging from 0.11 new species/My for the genus *Orbulina* to 1.44 new species/My for the keeled globorotalids of the Neogene. The rates determined for the foraminifers of the Olenekian are thus intermediate between the high rates for Cenozoic mammals and

planktonic foraminifers and the lower rates of Tertiary bivalves.

The highest extinction rates recorded, both for species and genera, are in the Olenekian, and these are the highest values of the Triassic with the exception of the Rhaetian extinction (Tables 1 and 2). This may be explained in several ways: the persistence of unfavourable environmental conditions (anoxia), which did not fully improve until the Anisian; the disappearance of Paleozoic species unable to compete with the newly emerging faunas; and finally, the emergence of many new unsuccessful species (Márquez and Trifonova, 2000). Throughout the Middle and Late Triassic, extinction rates decayed until they approached zero. This situation was to radically change in the Rhaetian, in which high rates are quoted both for genera and species (Márquez and Trifonova, 2000) (Tables 1 and 2, Figs. 2 and 3). Although outside the scope of this paper, an ample discussion of the Rhaetian extinction can be found in Márquez and Trifonova (2000).

The so-called “Lazarus” taxa probably contributed significantly to the recovery of Triassic fauna. Kozur (1998) indicated that among the different groups of organisms, especially those of the warm-water benthos (e.g., holoturians, scolecodonts, siliceous sponges, ostracods, bivalves and gastropods), 50% to 100% of the genera present in the Late Permian reappear during the Early to Middle Triassic. This timing of events is also applicable to the foraminifers (Table 3). Thus, of the 15 genera present in the Induan, 5 genera (33%) are Lazarus taxa that reappear during the Middle and Late Induan. During the Olenekian, of the 32 genera present, 8 genera are “Lazarus” taxa (25%), while of the 65 genera present in the Anisian, 9 reappeared (14%). Finally, during the Ladinian, only 2 of the 70 Permian genera present (3%) reemerged. If we consider overall data for the foraminiferal fauna of the Early–Middle Triassic, of the 86 genera present, 28% (24) already existed in the Paleozoic (Table 3). Moreover, this trend may be observed in every suborder of foraminifers of the Paleozoic and is particularly obvious for Textulariina, Miliolina and Fusulinina (Table 3). The presence of many “Lazarus” taxa seems to indicate that the marine ecosystems, or at least their foraminiferal faunas, did not attain true stability until millions of years had passed. This would explain the drop, from the Anisian onwards, in the rates of emergence of new

taxa as ecological niches, which had been free since the Permian, became occupied (Márquez and Trifonova, 2000). As these abnormal conditions improved, many taxa, which had managed to survive on the narrow shelves of oceanic islands in central warm-water areas within the tropical Panthalassa and the extensive eastern Tethys area, started to reoccupy the Tethyan tropical shelves in the Olenekian and Middle Triassic (Kozur, 1998).

### 5.3. Paleoeological and paleogeographical significance of the foraminiferal faunas of Iberia

The diversity of Triassic foraminifers in Iberia seems to be generally low. This could be because of the shallow marine facies, often restricted and ecologically highly unstable, associated with the position of

the Iberian plate in the westernmost Tethys. Associations are generally those typical of low energy, bay or lagoon type protected settings of a salinity sometimes higher than normal, on shallow carbonate ramps with a predominance of Ammodiscacea, Involutinacea, Duostominacea and some Nodosariacea.

The rich and diverse associations related to the reef complexes of the Sierra de Prades (Tarragona, Catalan Range) described in the previous section merit separate attention. The different reef facies include forms common to the Tethys such as *T. mesotriasica* (Koehn-Zaninetti), *P. meridionalis* (Luperto), *E. wirzi* (Koehn-Zaninetti), *D. alta* Kristan-Tollmann and *D. astrofimbriata* Fuchs, to mention a few. In these reef environments, the foraminiferal fauna is much more numerous and species diverse than in the carbonate ramps of the Triassic basins of Iberia.

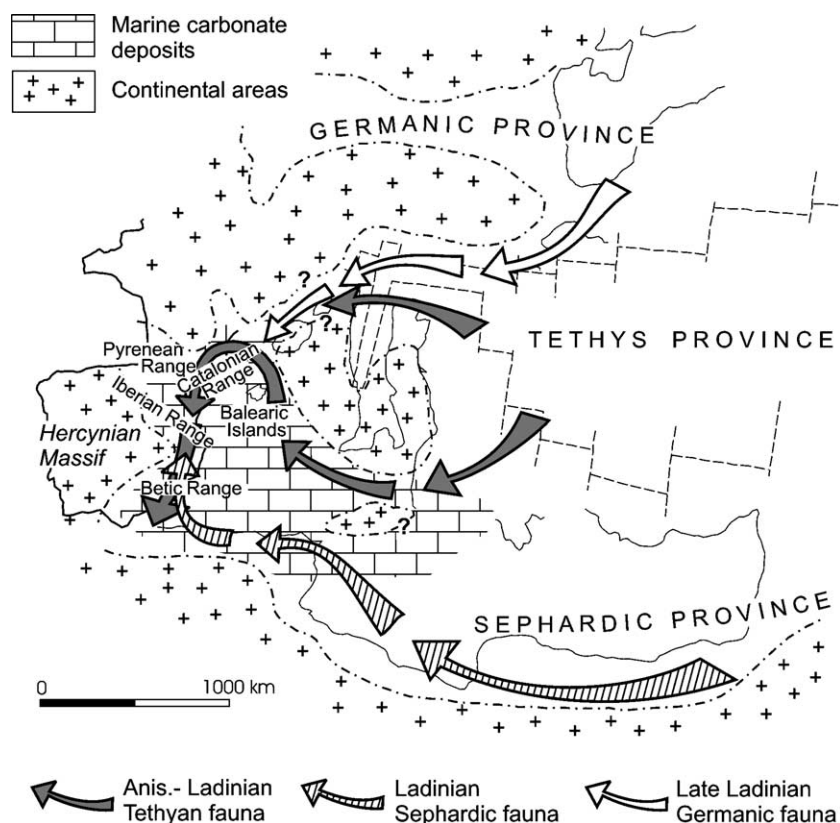


Fig. 6. Paleobiogeographical significance of the foraminiferal faunas of Iberia. Grey arrows indicate clear affinities in the Tethys province. Striped arrows show the presence of some Involutinina species in the Betic Range (Lower Ladinian) suggesting emigration from the Sephardic province (see text). Also note the species of Germanic affinities in NE Iberia during the Late Ladinian (Longobardian) (white arrows) (modified from Pérez-López et al., 2003a,b).

In paleogeographical terms, Iberia lay north of the equator in latest Permian–earliest Triassic times (Beauchamp and Baud, 2002) and was a significant entrance route during the westward propagation of the Tethys (Fig. 1). As in most of Central and Western Europe, Iberia was affected by the evolution of a complex of rift systems that were related to the initial break-up of Pangea, the southward propagation of the Norwegian–Greenland sea rift, as well as the development of the Tethys rift systems (Ziegler, 1988). These troughs did not develop simultaneously, such that the first transgression of the Tethys in Iberia during Anisian times unevenly covered different areas of the Iberian plate: the Iberian basin was the first to open during the Late Permian, followed by the Cantabrian–Pyrenean and Catalanian basins, and finally, it was probably not until the Middle–Late Triassic, that the Betic basin opened (López-Gómez et al., 1998).

Accordingly, it is important to consider the paleobiogeographic affinities of the Triassic foraminiferal faunas of Iberia. With the exception of some species of Nodosariidae and Spirillinidae of Germanic affinity that appear in a few sites in NE Iberia, most of the species present are widely known in the alpine Triassic. Therefore there seem to be no major differences with communities common from the Tethys, such that, as proposed by Budurov et al. (1993), we can consider the Spanish faunas as truly Tethyan (Fig. 6).

We should also mention the presence in the Betic Ranges Lower Ladinian of several species of Involutinina, well known in alpine basins during the Late Ladinian. The presence in Israel of similar associations in levels dated as Late Fasnian (Benjamini, 1988) seems to suggest the arrival of these species from the Sephardic domain during the Early Ladinian (Fasnian), which would later develop in alpine basins. This issue needs further analysis (Fig. 6).

## 6. Conclusions

- (1) The recovery of Triassic foraminiferal faunas in the western Tethys seemed to occur especially, but not exclusively, from species of Miliolina. The resulting associations were numerous and poorly diversified, formed mostly by cosmopolitan and eurifacial species.
- (2) Evolution rates indicate a delay at the levels of both genera and species in the recovery of foraminiferal faunas. Thus, maximum origination of new taxa rates were recorded for the Olenekian and Anisian. These rates subsequently approached zero when most of the ecological niches became reoccupied in the Ladinian and Late Triassic.
- (3) “Lazarus” taxa contributed greatly to the recovery of the Triassic foraminiferal faunas. Thus, out of all the genera present in the Early Triassic (Induan–Olenekian), 41% were genera that already existed in the Permian and reemerged after the extinction at the Permian–Triassic boundary. During the Middle Triassic (Anisian–Ladinian), this value was 14%. Overall, of all the genera present in the Early and Middle Triassic, 28% were “Lazarus” taxa. The reason for this behaviour, somewhat different from that inferred for stages subsequent to other mass extinctions, could be the persistence during the Early Triassic (Induan) of conditions unfavourable for marine life (anoxia?) across extensive zones of the Tethys, with normal conditions not being restored until the Olenekian.
- (4) In Iberia, the Lower Triassic is represented by continental facies (Buntsandstein) and thus the first foraminifer faunas are of Anisian age. The recovery of the Triassic fauna had largely taken place by that time, so that the associations appearing in Iberia for the Anisian are similar to those observed in other areas of the Tethys.
- (5) Paleoeologically, the Spanish Triassic foraminiferal faunas are generally comprised of poorly diversified communities showing an abundance of involutinids, nodosarids and some arenaceous forms and duostominids associated with the shallow environments of carbonate ramps, protected to a greater or lesser degree. Only in the Catalan Ranges do more diverse faunas linked to reef complexes appear.
- (6) Finally, from a paleobiogeographic standpoint, most of the Iberian faunas examined show clear “Tethyan” affinities. Also observed is the presence in the NE of Iberia of some species common in Germanic areas, as well as evidence of the possible arrival in the Betic basin of fauna from the Sephardic domain during the Ladinian.



This last point needs confirmation through a more detailed study.

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