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Survival and recovery of calcareous foraminifera pursuant to the end-Permian mass extinction

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Abstract

Ninety-one percent of calcareous foraminiferal genera became extinct during the end-Permian mass extinction. The Early Triassic Epoch was a survival phase characterized by a short-lived proliferation of disaster forms and then a prolonged interval of low diversity. The orders Miliolida and Lagenida experienced limited taxonomic re-diversification in Early and Late Anisian time, respectively. All fusulinoidean fusulinides became extinct in Late Permian time, and only two non-fusulinoidean genera persisted into the Early Triassic. Triassic fusulinides diversified to just five genera before the order became entirely extinct in Late Triassic time. Involutinides originated in Olenekian time from an unknown ancestor. They did not significantly diversify until Late Triassic time. **To cite this article:** *J.R. Groves, D. Altiner, C. R. Palevol 4 (2005)*.

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Résumé

Survie et reconquête des foraminifères calcaires après la crise biologique de la fin du Permien. Quatre-vingt-onze pour cent des foraminifères calcaires s'éteignent au cours de la crise biologique de la fin du Permien. Le début du Trias fut une période de survie caractérisée par une brève prolifération de « taxons désastre », à laquelle succéda un intervalle de temps prolongé de faible diversification. Les ordres des Miliolida et des Lagenida amorcèrent une re-diversification taxonomique limitée, respectivement au début et à la fin de l'Anisien. Tous les fusulinidés Fusulinoidea s'éteignirent à la fin du Permien, et uniquement deux fusulinidés non-Fusulinoidea persistèrent au début du Trias. Ces derniers ne donnèrent naissance qu'à cinq genres avant la disparition définitive de l'ordre, à la fin du Trias. Les Involutinida apparurent à l'Olenekien à partir d'un ancêtre inconnu. Leur diversification n'aura pas réellement lieu avant la fin du Trias. **Pour citer cet article :** *J.R. Groves, D. Altiner, C. R. Palevol 4 (2005)*.

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Mots clés : Foraminifères ; Crise biologique de la fin du Permien ; Reconquête triasique ; Ordre des Lagenida ; Ordre des Fusulinida ; Ordre des Miliolida ; Ordre des Involutinida

1. Introduction

The purpose of this contribution is to summarize the record of foraminiferal extinction, survival and recovery in strata bracketing the end-Permian mass extinction. Foraminifera comprise an immensely varied group [80] that ranges stratigraphically from Cambrian to Recent, occupies fresh water, brackish and marine aquatic environments, lives as infaunal and epifaunal benthos and as plankton, and ranges in size from less than 100 μm to over 10 cm. These unicellular organisms may be naked (rare) or possess a test that is organic (rare), siliceous (rare), agglutinated (common) or calcareous (common). Many types contain photosynthetic endosymbionts. In this review we limit our analysis to the calcareous secreted foraminifers that occurred abundantly in Late Paleozoic and Early Mesozoic neritic environments, especially carbonate facies, and whose taxonomy is reasonably well known. Late Paleozoic–Early Mesozoic agglutinated types are less commonly encountered in otherwise richly fossiliferous carbonate lithologies, and their taxonomy is still largely unsettled. The analysis is further limited to documented occurrences in the Upper Permian Wuchiapingian and Changhsingian stages through the Lower Triassic Induan and Olenekian stages. It focuses on changes in generic diversity within the orders Fusulinida, Miliolida, Lagenida and Involutinida.

Late Paleozoic calcareous foraminiferal assemblages were dominated by the Order Fusulinida, including a variety of large and internally complex forms. Early Mesozoic assemblages, in contrast, are characterized mostly by morphologically simple miliolides and lagenides. Planktonic forms originated in Jurassic time, and rotaliides, the dominant group of extant calcareous benthonic foraminifers, underwent their initial major expansion in Late Cretaceous time [7,84]. Clearly, the Permian–Triassic transition represents a critical period in foraminiferal evolutionary history insofar as the end-Permian mass extinction and pursuant survival and recovery intervals resulted in a dra-

matic turnover in the taxonomic composition of calcareous benthonic assemblages.

The cause(s) of the end-Permian mass extinction is (are) unknown and perhaps not knowable. Nevertheless, ongoing research has resulted in a wealth of information regarding the age of the Permian–Triassic boundary and the timing of unusual, possibly extinction-related circumstances relative to this date [6,22,61,63]. For instance, it is widely accepted that: (1) both shallow- and deep-water marine anoxia were widespread in Late Permian and Early Triassic time [41,42,98,101]; (2) a pronounced negative $\delta^{13}\text{C}$ excursion coincides or nearly coincides with the extinction horizon in both marine and non-marine sections worldwide [5,39,40,42,75,97]; (3) the eruptions of flood basalts in Siberia and felsic volcanics in South China were synchronous with the extinction, within experimental error [13,43,71,73,74]; (4) extinctions in the marine realm occurred quickly, possibly within ~500 kyr, during a rise in sea level [14,34,98,103]; and (5) the Permian–Triassic transition was a time of rapid and extreme global warming [48,60,76]. Viable extinction models must, at the very least, take into account these conditions [22], and these conditions necessarily also must have influenced the character and duration of the biotic recovery.

Previous reports on foraminiferal extinctions at the Permian–Triassic boundary include those by Brotzen [12], Brasier [7], Broglio-Loriga et al. [9], Broglio-Loriga and Cassinis [8], Tong [85], Hallam and Wignall [33], Rampino and Adler [70], Tong and Shi [86], Leven and Korchagin [52] and Groves et al. [30]. Early Triassic assemblages are less well known than Late Permian ones, and most information on them comes from the Tethyan region. Significant accounts of Tethyan Early Triassic foraminifers include those by Ho [37], Reitlinger [72], Efimova [19], Zaninetti [104], Trifonova [88,90], Yang and Jiang [102], Salaj et al. [81], Lin [54], He [35], He and Cai [36], and Rettori [77].

2. Earliest Triassic disaster forms

Fischer and Arthur [26 (p. 26)] defined disaster forms as “opportunistic species in the sense of MacArthur [58] and Levinton [53] [that] proliferated at times of biotic crises.” They noted that disaster forms bloom during episodes of overall taxonomic decline, so-called ‘oligotaxic’ periods, and they included the Permian–Triassic crisis among the eight most recent oligotaxic intervals. The most widely documented disaster forms pursuant to the end-Permian mass extinction were stromatolites and other microbially-influenced structures that flourished in an ecologically permissive time when grazing, bioturbation and skeletal production by normal marine benthos were greatly reduced [82], and when unusual marine chemistry may have promoted microbial calcification [78,79].

Basal Triassic deposits in many areas are devoid of foraminifers, but Hallam and Wignall [33] noted that in places large numbers of the morphologically simple, long-ranging, eurytopic foraminifer *Earlandia* immediately follow the end-Permian extinction. As such, Hallam and Wignall were the first to specifically identify an Early Triassic foraminiferal disaster form. *Earlandia* spp. were joined by the opportunistic miliolides *Cornuspira mahajeri* Brönnimann et al. [11] and/or *Rectocornuspira kalthori* (Brönnimann et al. [11]) to form depauperate assemblages in basal Triassic strata in Italy [11], Austria [45], Slovenia [69], Iran [11], Turkey [1,30,51,59,93] and China [25,99] (Fig. 1). In almost every instance, the *Earlandia*–*C. mahajeri*–*R. kalthori* assemblage occurs in microbialite facies or in close stratigraphic proximity to microbialites, reinforcing the interpretation of the assemblage’s constituents as disaster forms.

According to Hallam and Wignall [33] and Erwin [20,21], the presence of disaster forms is characteristic of the survival phase following a mass extinction. The subsequent disappearance of such forms, along with the proliferation of survivor and progenitor taxa and the reappearance of Lazarus taxa, marks the beginning of the recovery phase. In our experience (e.g., in Turkey and Italy), foraminiferal disaster blooms are present only in the basal few meters of the Griesbachian substage of the Triassic System. Their disappearance does not mark the beginning of foraminiferal recovery, however, as significant taxonomic expansion within most surviving orders did not occur until Anisian time or later.

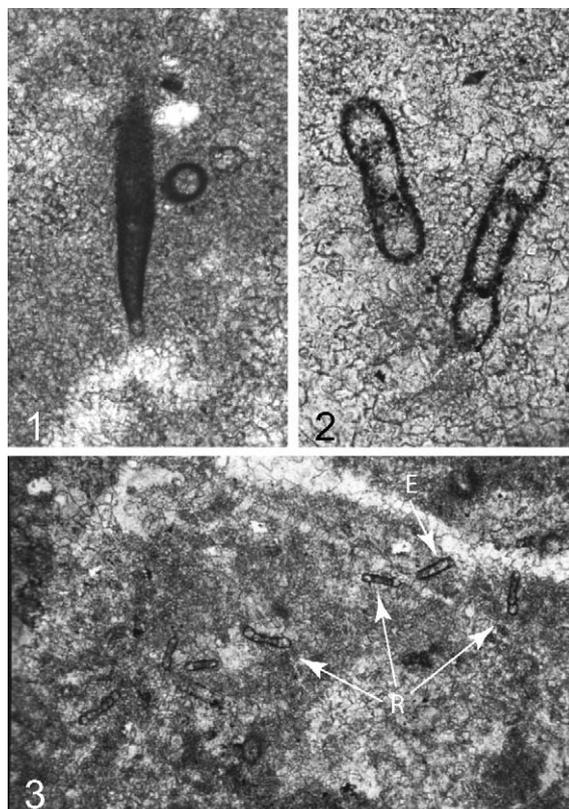


Fig. 1. Foraminiferal disaster forms in basal Triassic stromatolite facies, Central Taurides, Turkey. These forms occur in large numbers to the near exclusion of other taxa. **1**, *Earlandia* sp., longitudinal and transverse sections of two closely spaced individuals (Beslengiler Limestone Member of Sapadere Formation), $\times 100$; **2**, *Rectocornuspira kalthori* Brönnimann et al. [11], tangential axial sections of two closely spaced individuals (İspatli Member of Gevne Formation), $\times 200$; **3**, thin section print of multiple specimens of *R. kalthori* (R) and *Earlandia* sp. (E) (İspatli Member of Gevne Formation), $\times 50$.

Fig. 1. Foraminifères de type « taxons désastre » dans le faciès à stromatolites de la base du Trias, Taurides centrales, Turquie. Ces formes se rencontrent en grande quantité à la quasi-exclusion d’autres taxons. **1**, *Earlandia* sp., sections longitudinales et transversales de deux individus (Beslengiler Limestone Member de la formation Sapadere), $\times 100$; **2**, *Rectocornuspira kalthori* Brönnimann et al. [11], sections tangentielles axiales de deux individus (membre İspatli de la formation de Gevne), $\times 200$; **3**, lame mince montrant de nombreux exemplaires de *R. kalthori* (R) et d’*Earlandia* sp. (E) (membre İspatli de la Gevne Formation), $\times 50$.

3. Early Triassic survival and recovery

In this section we identify survivors of the end-Permian mass extinction and comment on the timing and taxonomic and paleobiogeographic characteristics

of the post-extinction survival and recovery phases. Calcareous foraminiferal genera in the orders Lagenida, Fusulinida, Miliolida and Involutinida from the Wuchiapingian through Olenekian stages are listed in Table 1, and changes in their diversity are depicted graphically in Fig. 2A. Total calcareous foraminiferal generic diversity for the same interval is shown in Fig. 2B.

3.1. Order Lagenida

Lagenides are calcareous benthic foraminifers whose walls are composed of low-Mg calcite in which the optical *c*-axes of crystal units are normal to the outer surface of the test, and in which the primary septal wall is monolamellar. Recent work suggests that the Order Lagenida is monophyletic [29,31,38,62], although in certain reference books [55] and previous analyses of foraminiferal diversity across the P–T boundary [86] a number of lagenide genera were regarded erroneously as either Fusulinida or Rotaliida, thus obscuring the actual ordinal-level record of extinction and survival.

Lopingian lagenides were diverse and abundant in inner to middle neritic environments throughout the Tethyan region and northern higher paleolatitudes [30]. At least 35 genera are known. Among them, *Geinitzina*, *Pachyphloia*, *Nodosinelloides*, *Protonodosaria* and *Robuloides* were especially widespread. Changhsingian strata in Turkey, Transcaucasia and China contain important occurrences of species that have been assigned to '*Dentalina*' and '*Nodosaria*', although specialists on Mesozoic and Cenozoic lagenides regard true *Dentalina* and *Nodosaria* as strictly Jurassic and younger genera.

Induan and Olenekian rocks contain very few lagenides, but the exact number of genera is difficult to assess because of taxonomic and nomenclatural uncertainties. The best documented faunas are from Turkey [30], Transcaucasia [19,72], Bulgaria [87,88,90] and China [35–37,54,102]. Lagenides in these reports include simple *Nodosaria*- and *Dentalina*-like forms with equant to elongate chambers that are circular in transverse section. At least two species, '*Nodosaria*' *hoae* (Trifonova [87]) and '*Nodosaria*' *elabugae* Cherdyntsev [15], are known also from older Changhsingian and younger Triassic strata, making them unquestioned survivors of the end-Permian extinction and the most likely rootstock for the later Triassic–Jurassic re-diversification of the lagenide clade. The uniserial

survivors were accompanied by non-septate syzraniids. Specimens assignable to *Syzrania* are known from the Lower Griesbachian of Turkey [30], and they were joined later in the Early Triassic and Middle Triassic by an additional non-septate form, *Tezaquina? luperti* (Efimova [19]), known from Turkey [30], Italy [56], Transcaucasia [19] and China [35].

Astacoline forms, interpreted as 'nodosariid' lagenides and described under *Astacolus*, *Lenticulina*, *Marginulina*, *Marginulinopsis*, *Saracenaria*, *Vaginulinopsis* and *Citharina*, have been documented from the Changhsingian–Griesbachian boundary interval in the Kashmir Himalaya (southern high paleolatitudes) by Kalia and Sharma [46] and Pande and Kalia [66]. These forms are poorly preserved and poorly illustrated, so confirmation of lagenide wall structure is difficult. If they are genuine lagenides, then all are probably assignable to one or two genera (*Astacolus* and/or *Eocristellaria*) and they may represent a distinct group of survivors that could have given rise to later recovery taxa. It is troubling, however, that astacoline forms are unknown elsewhere in Lower Triassic rocks.

Wignall and Newton [100] documented the local highest stratigraphic occurrences of *Pachyphloia*, *Geinitzina* (= their *Lunucammina*) and *Nodosaria*-like (= their *Lingulina*) lagenides in well-dated Griesbachian beds in southern Tibet. Similarly, we have observed *Geinitzina* and *Pachyphloia* specimens in unequivocal Griesbachian strata in the Southern Alps of Italy (JRG, unpublished observations). Wignall and Newton [100] interpreted the Tibetan occurrences as evidence for diachrony of the end-Permian extinction, suggesting that environmental deterioration responsible for the extinction did not reach the southern higher paleolatitudes until relatively late in Griesbachian time. If correct, this interpretation might account for the problematic Griesbachian occurrences of astacoline forms in the Kashmir Himalaya. Alternatively, Griesbachian occurrences of "Permian" lagenides in Tibet and Italy may simply represent stratigraphically reworked specimens or a few post-extinction holdovers that played no meaningful role in the subsequent recovery.

Thus, we conclude that Early Triassic lagenides comprised no more than four, but possibly only three genera or genus-group entities: morphologically simple, unquestioned Permian survivors that persisted into the later Triassic and undoubtedly figured prominently in

Table 1

Documented stratigraphic occurrences of Late Permian and Early Triassic calcareous foraminiferal genera

Tableau 1. Occurrences stratigraphiques documentées de genres de foraminifères calcaires de la fin du Permien et du début du Trias.

	Lopingian series		Lower Triassic series	
	Wuchiapingian stage	Changhsingian stage	Induan stage	Olenekian stage
Order Fusulinida				
<i>Abadehella</i>	×	×		
<i>Baudiella</i>		×		
<i>Boultonia</i>	×	×		
<i>Climacammina</i>	×	×		
<i>Codonofusiella</i>	×	×		
<i>Cribrogenerina</i>	×	×		
<i>Dagmarita</i>	×	×		
<i>Deckerella</i>	×	×		
<i>Earlandia</i>	×	×	×	×
<i>Endoteba</i>	×	×	?	×
<i>Endotebanella</i>				?
<i>Gallowayinella</i>	×	×		
<i>Globivalvulina</i>	×	×		
<i>Glomospiroides</i>	×	×		
<i>Lasiodiscus</i>	×	×		
<i>Lasiotrochus</i>		×		
<i>Louisettita</i>	×	×		
<i>Nankinella</i>	×	×		
<i>Nanlingella</i>	×	×		
<i>Neoendothyra</i>	×	×		
<i>Ogbinella</i>	×			
<i>Palaeofusulina</i>	×	×		
<i>Palaeonubecularia</i>	×	×		
<i>Palaeotextularia</i>	×	×		
<i>Paradagmarita</i>		×		
<i>Paradunbarula</i>	×	×		
<i>Paraglobivalvulina</i>	×	×		
<i>Paraglobivalvulinooides</i>		×		
<i>Parananlingella</i>	×	×		
<i>Parareichelina</i>	×	×		
<i>Polytaxis</i>	×	×		
<i>Postendothyra</i>	×	×		
<i>Pseudodunbarula</i>	×	×		
<i>Pseudovidalina</i>	?			
<i>Reichelina</i>	×	×		
<i>Schubertella</i>	×			
<i>Septoglobivalvulina</i>	×	×		
<i>Sichotenella</i>		×		
<i>Sphaerulina</i>	×	×		
<i>Spireitlina</i>	×	×		
<i>Staffella</i>	×	×		
<i>Tetrataxis</i>	×	×		
<i>Tewoella</i>	×	×		
<i>Urushtenella</i>		×		

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Table 1
(continued)

	Lopingian series		Lower Triassic series	
	Wuchiapingian stage	Changhsingian stage	Induan stage	Olenekian stage
Order Lagenida				
<i>Astacolus</i>		×	?	
<i>Calvezina</i>	×	×		
<i>Colaniella</i>	×	×		
<i>Cryptomorphina</i>	×	×		
<i>Cryptoseptida</i>	×	×		
' <i>Dentalina</i> '	×	×	×	×
<i>Eocristellaria</i>	×	×	?	
<i>Fronicularia</i>	×	×		
<i>Fronidina</i>	×	×		
<i>Froninodosaria</i>	×	×		
<i>Geinitzina</i>	×	×		
<i>Gourisina</i>		×		
<i>Hubeiroluloides</i>		×		
<i>Ichthyofronidina</i>	×	×		
<i>Involutaria</i>		×		
<i>Langella</i>	×	×		
<i>Neogeinitzina</i>	×	×		
" <i>Nodosaria</i> "	×	×	×	×
<i>Nodosinelloides</i>	×	×		
<i>Olympina</i>		×		
<i>Pachyphloia</i>	×	×		
<i>Paracolaniella</i>		×		
<i>Protonodosaria</i>	×	×		
<i>Pseudocolaniella</i>		×		
<i>Pseudoglandulina</i>	×	×		
<i>Pseudolangella</i>	×	×		
<i>Pseudonodosaria</i>		×		
<i>Pseudotristix</i>	×	×		
<i>Rectoglandulina</i>		×		
<i>Rectostipulina</i>	×	×		
<i>Robuloides</i>	×	×		
<i>Robustopachyphloia</i>	×	×		
<i>Syzrania</i>	×	×	×	
<i>Tauridia</i>	×	×		
<i>Tezaquina?</i>			×	×
<i>Tristix</i>		×		
<i>Vervilleina</i>	×	×		
Order Miliolida				
<i>Agathammina</i>	×	×	?	?
<i>Apterinella</i>	×	×		
<i>Baisalina</i>	×	×		
<i>Cornuspira</i>	×	×	×	?
<i>Hemigordius</i>	×	×		
<i>Kamurana</i>		×	×	
<i>Multidiscus</i>	×	×	?	
<i>Neodiscus</i>	×	×		

(continued on next page)

Table 1
(continued)

	Lopingian series		Lower Triassic series	
	Wuchiapingian stage	Changhsingian stage	Induan stage	Olenekian stage
<i>Neohemigordius/Arenovidalina</i>	×	×	?	×
<i>Nikitinella</i>	×	×		
<i>Plummeriella</i>	×	×		
<i>Ramovsia</i>	×	×		
<i>Rectocornuspira</i>	×	×	×	
<i>Septagathammina</i>	×	×		
<i>Streblospira/Meandrospira</i>	×	×	?	×
streptospiral cornuspirid	×	×		
streptospiral hemigordiopsid	×	×		
Order Involutinida				
<i>Triadodiscus</i>				×

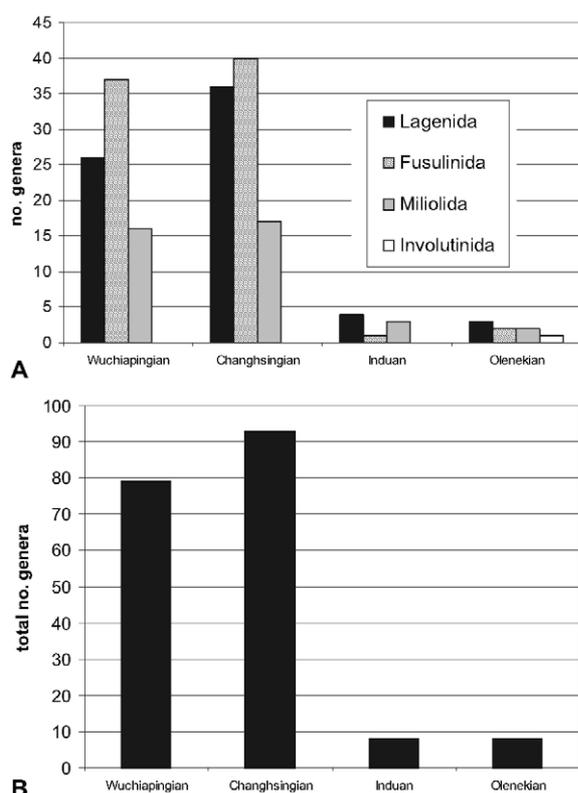


Fig. 2. Late Permian to Early Triassic calcareous foraminiferal generic diversity. **A**, generic diversity by orders; **B**, total generic diversity.

Fig. 2. Diversité générique des foraminifères calcaires à la fin du Permien et au début du Trias. **A**, diversité générique par ordres ; **B**, diversité générique totale.

the lagenide recovery (syzraniids; *Nodosaria*-like; *Dentalina*-like), and astacolone forms whose status as survivors and whose role in the recovery remains unclear. There is no evidence among documented Early Triassic faunas for the survival of taxa with more derived features such as laterally compressed or subdivided chambers, radiate or otherwise highly modified apertures, or secondary lamellarity of the wall. The reappearance of such features in later Triassic and younger taxa is attributed to convergence, and this accounts for the many instances of Elvis taxa [23] among Paleozoic and Mesozoic-Cenozoic lagenides. We know of no Lazarus taxa.

Elsewhere [30], in an attempt to gauge the onset of recovery, we estimated lagenide species diversity within Triassic substages through the Middle Triassic Series (Fig. 3). Species diversity during Griesbachian time was approximately 9, or less than one-tenth that of the Changhsingian Stage, underscoring the catastrophic decline suffered by lagenides during the end-Permian extinction. Species numbers remained low, hovering at or below 11, for the remainder of the Lower Triassic Series and then increased to only 16 by the end of the Pelsonian Substage of the Anisian Stage. The first marked pulse of species diversification occurred in Illyrian time, about 15 Myr after the extinction, when numbers almost doubled to 28. Ladinian species numbers nearly doubled again (45–46), indicating that by the end of Middle Triassic time lagenides were becoming speciose, although they did not re-establish pre-extinction levels of diversity until the Late Triassic or Early Jurassic. Thus, in the aftermath of the end-Permian extinction, lagenides experienced an extremely protracted survival interval characterized by little diver-

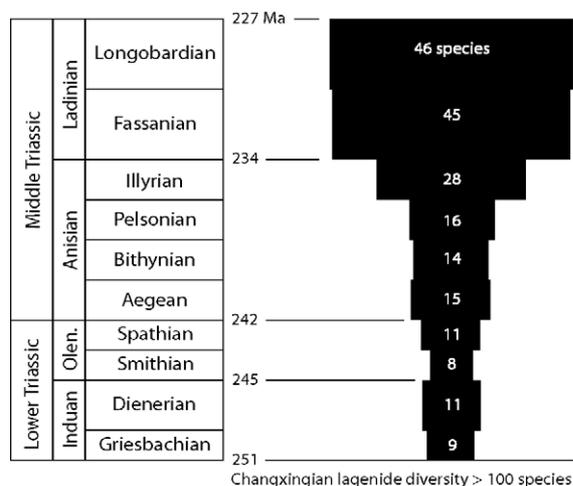


Fig. 3. Protracted survival of lagenide species pursuant to end-Permian mass extinction. Main pulse of re-diversification began in Late Anisian (Illyrian) time, ~15 Myr after the Permian–Triassic boundary. Vertical scale is time-linear, with absolute ages from International Commission on Stratigraphy (International Union of Geological Sciences; <http://www.micropress.org/stratigraphy/>). Data from Groves et al. [30].

Fig. 3. Progression au cours du temps de la survie des espèces chez les lagénidés après les extinctions massives de la fin du Permien. L'étape majeure de la re-diversification débute au cours de l'Anisien supérieur (Illyrien), 15 millions d'années après la limite Permien–Trias. L'échelle verticale des durées est proportionnelle au temps, les âges absolus étant ceux définis par la Commission internationale de stratigraphie (International Union of Geological Sciences ; <http://www.micropress.org/stratigraphy/>). Données d'après Groves et al [30].

sification at the genus or species level. True recovery did not begin until Late Anisian time and it may have extended through the end of the Triassic, in distinct contrast to certain invertebrates whose combined survival and recovery phases lasted 5–8 Myr [21,24,91].

3.2. Order Fusulinida

The Order Fusulinida is the only major group of foraminifers with no living representatives [83]. All fusulinides possessed a homogeneously microgranular primary test wall of low-Mg calcite in which crystal units are optically unordered, more or less equidimensional, and only a few micrometres in size. [Fusulinoidean fusulinides of the Family Staffellidae are usually recrystallized, suggesting that they secreted an aragonite or high-Mg calcite wall.] Because a standard petrographic thin section is ~30 µm thick, sections through

fusulinide walls contain many crystal interfaces at which light is internally reflected and refracted, resulting in the characteristic dark appearance. The walls in various representatives of the order contain adventitious grains, layering as a consequence of secreted microgranular or hyaline-radial secondary deposits, or fine to coarse pores.

According to Tappan and Loeblich [84], the order comprises 418 distinct genera, not including subjective synonyms or subsequently erected new genera. Clearly, fusulinides were the dominant group of calcareous secreted foraminifers of the Paleozoic Era, with the main superfamilies Endothyroidea and Fusulinoidea achieving their peak diversities during Viséan and Cisuralian times, respectively. The initial decline of fusulinoideans coincident with the end-Guadalupean extinction eliminated all large and morphologically complex forms assignable to the Schwagerinidae and Neoschwagerinidae [52], so that only 15 genera in the families Schubertellidae and Staffellidae persisted into Lopingian time. An additional 23 to 25 genera of non-fusulinoidean fusulinides are known from Wuchiapingian and Changhsingian rocks, respectively. Of these, the most abundant and speciose belonged to the families Biseriamminidae, Endothyridae, Tetrataxidae, Palaeotextulariidae and Lasiodiscidae.

No fusulinoideans are known to have survived the end-Permian extinction. Authors of older literature concerning the existence of non-fusulinoidean fusulinides in Triassic rocks were polarized in two camps: those who regarded all fusulinides to have become extinct prior to the Triassic Period [55,84]; and those who employed 'Paleozoic' names such as *Haplophragma*, *Endothyra*, *Endothyranella*, *Neoendothyra* and *Tetrataxis* for Triassic specimens [10,81]. We concur with the more recent assessment of Rettori [77], who recognized the endothyroideans *Endoteba*, *Endotebanelle*, *Endotriada* and *Endotriadella* as true fusulinides in Triassic strata in the Tethyan region. Certain of these forms are convergent with strictly Paleozoic taxa, perhaps accounting for disparate opinions regarding fusulinide survival across the P–T boundary. To this list we add the morphologically simple, long-ranging *Earlandia*, which is known to occur in large numbers as a 'disaster form' in basal Triassic deposits, and which is reported to have experienced a very modest species-level diversification in Middle Triassic time before suffering Late Triassic extinction [33].

The type species of *Endoteba*, *E. controversa* Vachard and Razgallah [94], is known from Upper Permian rocks in Tunisia, Yugoslavia, Italy, Afghanistan and Japan [77]. Curiously, according to Rettori [77], Triassic occurrences of this species and its congeners are known almost exclusively from Anisian and younger deposits throughout the Tethyan region, with the only documented Early Triassic occurrence being that of *E. ex gr. bithynica* Vachard et al. [95] in Upper Skythian (= Olenekian) strata of northwest Turkey [17,18]. Thus, by virtue of having no known Induan occurrences, *Endoteba* is regarded as a Lazarus taxon. None of the other Triassic fusulinides is known from the Permian, and apparently none survived beyond the Triassic. *Endotebanella* (uppermost Olenekian or lower Anisian through Carnian) is a presumed evolutionary derivative of *Endoteba*, whereas *Endotriada* and *Endotriadella* (both Middle Triassic) may have derived from *Neoendothyra* or *Endoteba* [77]. None of the Triassic fusulinide genera is speciose: in the Tethys, *Endoteba* was represented by four species or species-groups; *Endotebanella*, *Endotriada* and *Endotriadella* were represented by a single species each.

Ünal [92] reported supposedly in situ biserialminid fusulinides from basal Triassic beds in the Hadim region of the Central Taurides, Turkey. We have seen similar occurrences in the nearby Taskent region [JRG unpublished observations], but we regard the Triassic biserialminids as either stratigraphically reworked from underlying Upper Permian beds in which they are common, or as local survivors that failed to persist beyond Earliest Griesbachian time.

In summary, two genera of fusulinides (*Earlandia*, *Endoteba*) survived the end-Permian mass extinction, but they never experienced significant taxonomic recovery. Minimal post-extinction expansion resulted in peak Middle Triassic diversity of five genera and probably no more than ten species. The fusulinide clade became entirely extinct in Late Triassic time.

3.3. Order Miliolida

Foraminifers in the Order Miliolida are characterized by porcelaneous tests of high-Mg calcite in which small rod-like crystals are randomly oriented. The tests are milky opaque in reflected light and brown in transmitted light. Miliolides first appeared at the beginning

of Pennsylvanian time and then proliferated in Middle and Late Permian time following the Capitanian transgression in the Tethyan realm [4].

The order includes many ecologic generalists and opportunists [47] that normally existed in low numbers, but which bloomed during environmental crises. These taxa are mainly cornuspirins (*Cornuspira*, *Rectocornuspira*, *Agathammina*, *Agathamminoides*), meandrospirins (*Streblospira*) and attached calcivertellins (*Apterrinella*, *Plummeriella*). The most diverse Permian representatives of the order are hemigordiopsids and baisalinids. Among the hemigordiopsids, forms with axially thickened shells and variable coiling (*Hemigordius*, *Neodiscus*, *Multidiscus*) gave rise in Middle Permian time to relatively larger forms with reduced chamber heights (*Hemigordiopsis*, *Lysites*) and others whose chamber cavities are occupied by pillars (*Shanita*). Other morphologic trends included the origination of lenticular forms with thickened umbilical regions (*Neohemigordius*) and large, completely streptospiral forms (*Hemigordius sensu lato*). Middle Permian baisalinids possessed incomplete division of the tubular chamber by rudimentary septa or complete partitioning by true septa. These variably septate miliolides probably evolved in at least three different lineages (*Nikitinella*, *Baisalina*, *Pseudobaisalina*). The sporadically occurring generalist/opportunist taxa, hemigordiopsids, and baisalinids comprised at least 19 genera in Capitanian time, the peak of miliolide diversity during the Paleozoic Era.

The causes of end-Guadalupian extinctions, which claimed the morphologically complex fusulinoids, also appear to have affected the Miliolida, although there is uncertainty with respect to the stratigraphic ranges of certain genera. Morphologically complex genera, such as *Hemigordiopsis*, *Lysites*, *Shanita* and the specialized baisalinid *Pseudobaisalina*, seem to have been eliminated. Less complicated and ecologically more tolerant forms persisted.

Wuchiapingian and Changhsingian miliolide associations exhibit stable and roughly equal generic diversity, except for the appearance of *Kamurana* in the Changhsingian [2,49,50,57]. The end-Permian extinction then nearly eliminated the order, as almost all hemigordiopsids and baisalinids disappeared [1,2,16,27,32,33,44,50,51,64,70,93,96]. The extinction of the order was not complete, however, as certain cornuspirins (*Cornuspira*, *Rectocornuspira*) occur just above the

Permian–Triassic boundary [77,104], apparently because of tolerance for environmental stress. The paleobiogeographic distribution of these short-lived disaster forms is confined to the western Tethyan area including Italy, Hungary, Yugoslavia, Bulgaria, Austria, Turkey and Iran [77]. The Permian genus *Kamurana* survived in the Early Triassic of Bulgaria where it is represented by a single species [89], which we regard as a failed crisis progenitor taxon [47].

The miliolide survival interval spanned all of Early Triassic time, with taxonomic expansion delayed until the Anisian Stage. We interpret the genus *Meandrospira* as a Lazarus taxon whose occurrences in the Olenekian Stage probably represent the phyletic continuation of Permian forms assigned to *Streblospira*. Intervening Induan populations are not known, possibly because of taphonomic bias or retreat into refugia. *Meandrospira* underwent modest but biostratigraphically important species-level diversification beginning in the Early Anisian [77,104]. The genus *Agathammina* also could be considered a Lazarus taxon. Permian occurrences are well documented, but the next higher occurrences are upper Middle Triassic or Upper Triassic, suggesting prolonged residence in refugia. Alternatively, it is possible that the Permian and Triassic *Agathammina* are homeomorphs (Elvis taxa). Evolution similar to the *Streblospira-Meandrospira* continuum apparently also took place in the *Neohemigordius-Arenovidalina* lineage, as suggested previously by Zaninetti et al. [106] and Zaninetti and Martini [105]. *Arenovidalina*, then, could be regarded as a Lazarus taxon that appeared in the Olenekian and gave rise later in the Mesozoic to a large group of porcelaneous foraminifers known as ophthalmidiids.

3.4. Order Involutinida

This order is characterized by an enrolled tubular second chamber with lamellar thickenings or pillar-like structures in the umbilical region of one or both sides of the test. The wall is aragonitic but commonly recrystallized to a homogenous microgranular structure. The oldest representative of the order is *Triadodiscus*, which seems to have appeared in the late Early Triassic (Olenekian) [28,68,77] with no known Induan occurrences. The genera *Neohemigordius* and *Pseudovidalina* were erroneously included in the order by Loeblich and Tap-

pan [55]. *Neohemigordius* is a hemigordiopsid miliolide and possibly a junior synonym of *Hemigordius* [4], whereas *Pseudovidalina* is a fusulinide [3].

The abrupt Olenekian appearance of the earliest involutinides suggests that the ancestor of the order could be found among Permian taxa. One of the most commonly cited hypotheses is a possible archaediscacean origin [28,65,68,81]. True archaediscaceans, however, are confined to the Mississippian through lower Middle Pennsylvanian and have never been recorded in the Permian. Archaediscacean-like pseudovidalinids are present in the Middle to Upper Permian, but they are not likely ancestors of the Triassic Involutinida because the pseudovidalinids seemingly never modified their wall structure pursuant to their first appearance in the upper Middle Pennsylvanian. Separately, Gargouri and Vachard [27] proposed their porcelaneous '*Glomospirella*' as a possible ancestor of the Involutinida. One of us [DA] favors an alternate hypothesis in which the hemigordiopsid *Multidiscus* could have given rise to involutinides. As pointed out by Altiner et al. [4], the genera *Neodiscus* and *Multidiscus* are highly derived hemigordiopsids with radially arranged fibrous structures in their otherwise miliolide walls. This presumed synapomorphic feature would link *Neodiscus* and *Multidiscus* with the Involutinida, with *Multidiscus* being the most likely ancestor owing to its entirely planispiral coiling. *Multidiscus* is not definitely known from the Earliest Triassic, however, so this scenario requires an Induan residence in refugia where the *Multidiscus-Triadodiscus* transition could have occurred via transformation of the wall mineralogy from high-Mg calcite to aragonite. Counter to this hypothesis, it must be pointed out that the involutinide test wall is made up of hyaline-fibrous crystal units that are secreted *in situ* on an organic substrate. This differs significantly from the formation of the miliolide wall in which crystallites are secreted intracellularly and then transported to the cell periphery by Golgi vesicles. Moreover, rDNA analyses suggest major separation between miliolides and other testate foraminifera [67], further diminishing the likelihood of a genealogic link between them and involutinides.

Regardless of their ancestry, involutinides diversified during Middle and Late Triassic time. Several evolutionary trends are recognizable and biostratigraphically useful in delineating the Norian and Rhaetian stages [68,104].

4. Conclusions

- (1) Ninety-three genera of calcareous foraminifers are known in Upper Permian (Changhsingian) strata worldwide, although most occurrences are from the Tethyan realm. Eighty-five of these failed to survive the end-Permian mass extinction, resulting in a generic extinction rate of 91%. The eight surviving genera do not include equivocal Early Triassic occurrences or inferred occurrences of suspected Lazarus taxa.
- (2) Generic diversity in the orders Lagenida, Fusulinida and Miliolida exhibited similar patterns in the Lopingian and Early Triassic epochs. In each group, diversity increased slightly from Wuchiapingian to Changhsingian time before crashing at the Permian–Triassic transition. The entire Early Triassic Epoch was a survival interval characterized by the transient proliferation of disaster forms and then a period of very low overall generic diversity.
- (3) Post-extinction re-diversification marks the end of the survival phase and the beginning of the recovery phase. Miliolide and lagenide foraminifers experienced modest expansion in Early and Late Anisian time, for protracted survival intervals lasting ~9 Myr and ~15 Myr, respectively. Recovery was protracted as well, as neither group achieved pre-extinction levels of generic diversity until Late Triassic time.
- (4) Fusulinides, the dominant calcareous foraminifers of the Paleozoic Era, never recovered following the end-Permian mass extinction. Fusulinoidean fusulinides were eliminated coincident with the erathem boundary. Only two genera of non-fusulinoidean fusulinides are definitely known in Lower Triassic strata, and only three additional genera appeared in the Middle Triassic. The order ultimately became extinct in Late Triassic time.
- (5) Involutinide foraminifers appeared in Olenekian time, although their ancestry is unclear. They underwent diversification in Late Triassic time.

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