

TRENDS IN DIVERSITY, SIZE, AND COMPLEXITY OF TRIASSIC FORAMINIFERA

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Associate Editor: Maria Rose Petrizzo.

To cite this article: Gale L. (2026) - Trends in diversity, size, and complexity of Triassic Foraminifera. *Rivista Italiana di Paleontologia e Stratigrafia*, vol. 132(3): 655-671.

Keywords: Macroevolution; recovery; diversification; larger benthic foraminifera; endosymbiosis.

Abstract: Trends in the diversity, size, and complexity of Triassic foraminifera were studied. Diversity was quantified as number of species and as mean standing diversity. Maximum linear dimensions were taken as approximations of size. As per complexity, foraminifera were graded based on test architecture and wall features. Foraminiferal diversity continually increased through the Triassic, but at a slower pace after the middle Anisian. The lower size limit of foraminifera does not change. The upper size limit and the mean size greatly increased in the early Anisian but remained constant afterward. The expansion of the size range suggests diversification into new niches and/or release from environmental pressure. The average size lies closer to the lower size limit, which suggests that small size is advantageous for some foraminifera, or that smaller species produce more evolutionary offspring. The most complex foraminifera in the Early Triassic – Anisian are multilocular. An exception is *Kamurana chatalovi*, which inherited a coarsely perforated wall from its Permian antecessors. New taxa with endoskeleton appeared during the Ladinian. Additional internal structures increase the strength of the test and may have allowed some lineages to expand into high-energy environments. During the Carnian, several miliolid genera with thick porcelaneous walls and coarse perforations appeared. In the Norian and Rhaetian, coarse perforations are also known in hyaline *Involutina* and *Aulosina*. Perforations could ease gas exchange or could be related to the acquisition of symbiotic algae in relation to the spreading of oligotrophic conditions and/or the evolution of suitable endosymbionts.

INTRODUCTION

Foraminifera (kingdom Protozoa, infrakingdom Rhizaria; Cavalier-Smith 2004) are a group of eukaryotic testate protists characterized by a network of granular pseudopodia, a complex alternation of haploid and diploid generations, and a test wall, which may be organic, agglutinated and/or made of secreted calcium carbonate, and rarely

silica (Loeblich & Tappan 1964; Sen Gupta 1999; BouDagher-Fadel 2008; Mikhalevich 2014). Whereas the group probably originated in the Neoproterozoic (Pawłowski et al. 2003; Groussin et al. 2011), the earliest foraminifera with agglutinated walls come from Cambrian rocks (Culver 1994; McIlroy et al. 2001), and the fossil record of foraminifera expands profoundly in the younger periods, offering a continuous view into their evolution (Morard et al. 2022). Approximately 9,000 recent species are currently known (Hayward et al. 2026), most from the marine environment and most being benthic

Received: February 05, 2026; accepted: September 10, 2026

(Morard et al. 2022). In addition, approximately 41,000 fossil species have been recognized as of 2026 (Hayward et al. 2026).

Foraminiferan macroevolution has been studied from different points of view. Examples include longevity in species of benthic foraminifera (Buzas-Stephens et al. 2025), tempo and mode of speciation in planktic foraminifera (Thunell 1981; Stanley et al. 1988; Hull & Norris 2009; Strotz & Allen 2013; Pearson & Ezard 2014; Tadir et al. 2021), repetitive recruitment of planktic foraminifera from benthic ancestors (Caron & Homewood 1983; Keller 1988; Hart et al. 2003; Arenillas & Arz 2017; Morard et al. 2022), the acquisition of algal symbiosis and the evolution of symbiont-bearing benthic foraminifera (Lee et al. 1979; Prazeres & Renema 2019), evolution in the test size in foraminifera (Kaiho 1999; Payne et al. 2012), evolution of dwarfism during prolonged periods of environmental stress (MacLeod 1990; Keller & Abramovich 2009; Wade & Olsson 2009; Song et al. 2011; Omaña et al. 2012; D'Onofrio et al. 2024), long-term trends in complexity (Brasier 1982a, b; Septfontaine 2020), and recovery of foraminiferan assemblages after the extinction events (Tur 1996; Alegret et al. 2009; Payne et al. 2011; Feng et al. 2024).

The macroevolution of Triassic foraminifera is bounded by two mass extinction events: the Permian/Triassic boundary extinction, and the Triassic/Jurassic boundary extinction (Raup & Sepkoski 1982; Bambach 2006). Extensive volcanism is the presumed cause of both extinctions, with global warming and ocean acidification among the chief environmental impacts (Wignall 2001; Schoepfer et al. 2022; Wignall & Bond 2024). At present, less is known about the Carnian biotic turnover, which was presumably also related to volcanic activity (Simms & Ruffel 1989; Miller et al. 2017; Dal Corso et al. 2020), but Li et al. (2025) found no significant extinction among Carnian foraminifera in China.

Numerous studies of recovery patterns have focused on foraminiferan evolution during the Permian/Triassic boundary mass extinction and its immediate aftermath (Brotzen 1963; Brazier 1988; Broglio Loriga et al. 1988; Broglio Loriga & Cassinis 1992; Tong & Shi 2000; Leven & Korchagin 2001; Groves & Altiner 2005; Márquez 2005; Groves et al. 2005, 2007; Song et al. 2007, 2009; Nestell et al. 2011; Payne et al. 2011; Korngreen et al.

2013; Song et al. 2015; Feng et al. 2020; Altiner et al. 2021; Yang et al. 2024; Nagy et al. 2026). These works show that the extinction severely diminished calcareous foraminifera (Leven & Korchagin 2001; Groves & Altiner 2005; Groves et al. 2005; Song et al. 2009), as well as agglutinated taxa (Song et al. 2009). The extinction particularly affected large and architecturally complex taxa, so that only morphologically simpler taxa survived into the Early Triassic (Brazier 1988; Leven 1998; Leven & Korchagin 2001; Yang et al. 2004; Groves & Altiner 2005; Song et al. 2009). A single species *Kamurana chatalovi* Trifonova, 1984 from the Lower Triassic of Bulgaria represents an exceptional case of the survival of a more complex Permian genus with a perforated porcelaneous wall (Trifonova 1984). Following the Permian/Triassic boundary extinction and an Early Triassic low in diversity, the number of foraminiferan taxa gradually increased by the end of the Anisian (Tappan & Loeblich 1988; Tong & Shi 2000; Leven & Korchagin 2001; Groves & Altiner 2005; Groves et al. 2005; Altiner et al. 2021). The recovery of diversity is mirrored by the trend in the upper size range of foraminifera: a significant drop in foraminiferal sizes at the beginning of the Triassic (Song et al. 2011; Payne et al. 2011; Rego et al. 2012; Schaal et al. 2016; Feng et al. 2020; Yang et al. 2024) is followed by a progressive increase during the recovery phase (Payne et al. 2011; Rego et al. 2012). No large-scale changes in size have been observed after the Anisian (Rego et al. 2012; Schaal et al. 2016; Feng et al. 2020), although Rego et al. (2012) noted an increase in size among the involutinids within the Norian–Rhaetian, and a decrease in size in *Galeanella* during the Carnian–Norian interval. According to Rego et al. (2012), the Permian/Triassic boundary reduction in size was principally governed by a reduction in size within surviving taxa rather than by the selective extinction of larger taxa, and the increase in size during the recovery interval was led by an increase in size within survivors and the extinction of the smallest species, rather than the origination of new larger taxa. Ocean hypoxia/anoxia, ocean acidification, global warming, lower availability of food, and a release from the pressure of competitors and predators have all been offered as possible explanations for the Early Triassic reduction in size in foraminifera (Payne et al. 2011; Song et al. 2011; Rego et al. 2012; Feng et al. 2020; Song et al. 2024; Yang et al. 2024).

Stage	Substage	No. genera	No. species	No. agg.	No. calc.	No. hyal.	Nbt	NFt	NBl	Nsin	Nt	Nb	Nstand
Induan	Griesbachian	12	13	2	3	8	4	6	0	3	10	4	7
	Dienerian	15	21	9	4	8	10	11	0	0	21	10	15.5
Olenekian	Smithian	25	38	14	12	12	17	11	4	6	28	21	24.5
	Spathian	36	63	24	18	22	19	28	9	7	47	28	37.5
Anisian	Aegean	60	122	40	30	49	40	71	7	4	111	47	79
	Bithynian & Pelsonian	70	149	55	44	49	103	28	5	13	131	108	119.5
	Ilyrian	86	215	63	56	96	87	49	44	34	136	131	133.5
Ladinian	Fassanian	79	190	45	55	90	129	43	7	11	172	136	154
	Longobardian	81	195	45	54	96	149	17	23	6	166	172	169
Carnian		105	297	67	82	148	108	72	57	59	180	165	172.5
Norian		112	272	70	67	135	146	71	35	20	217	181	199
Rhaetian		120	403	75	57	271	/	/	/	/	149	217	183

Tab. 1 - Raw numbers of diversity, range-through, extinct and newly evolved species, and normalized diversity at the subage level for the Triassic. No. agg: number of agglutinated species; No. calc.: number of calcareous species; No. hyal.: number of hyaline species; Nbt: number of range-through species; NFt: number of only top boundary-crossing species; NBl: number of only bottom boundary-crossing species; Nsin: number of singletons (confined to interval) species; Nt: total number of top boundary-crossing species; Nb: total number of bottom boundary-crossing species; Nstand: mean standing diversity. Note that the data for the Rhaetian is incomplete because the Jurassic material was not included in the study.

The aim of this study is to complement previous observations of the diversity and trends in size with an independent study based on the survey of the literature encompassing the entire Triassic Period. In addition to diversity and size, we analyze the architectural complexity of Triassic foraminifera by categorizing them according to the number of chambers, elements of the endoskeleton, and the presence of unique features in the wall (a rudimentary exoskeleton), which opens up a new view on the macroevolution of benthic foraminifera during the Triassic.

MATERIAL AND METHODS

Biodiversity

The presented analysis is based on a survey of 106 literature sources published between 1951 and 2025 (Supplementary Table S1). Altogether, the sizes of 759 species from 201 genera were determined at the stage or substage level from the Induan to the Rhaetian (Table 1; Supplementary Table S2). The stratigraphic intervals considered thus comprise: Griesbachian, Dienerian, Smithian and Spathian substages of the Induan and Olenekian, Aegean, combined Bithynian and Pelsonian, and Ilyrian substages of the Anisian, Fassanian and Longobardian substages of the Ladinian, and Carnian, Norian, and Rhaetian stages (Fig. 1). Pooling part of the data at the stage level was unavoidable due to excessively low stratigraphic resolution in the literature for the mid Anisian, Carnian, Norian, and Rhaetian stages.

Fig. 1. Chronostratigraphic/geo-chronological subdivision of the Triassic. After Cohen et al. (2025).

System/Period	Series/Epoch	Stage/Age	Substage/Subage	Duration (Myr)
TRIASSIC	Upper	Rhaetian		4.3
		Norian	Sevatian	21.6
			Alaunian	
			Lacian	
		Carnian	Tuvalian	9.7
			Julian	
	Middle	Ladinian	Longobardian	4.5
			Fassanian	
		Anisian	Ilyrian Pelsonian Bithynian Aegean	5.2
	Lower	Olenekian	Spathian Smithian	3.2
		Induan	Dienerian Griesbachian	2

The foraminiferan genus *Earlandia* (= *Aeolis-sacus*) was also included in the analysis, despite its uncertain taxonomic position (Golubic et al. 2006). Where disagreements appeared in terms of the validity of some taxa, the World Foraminifera Database was consulted (Hayward et al. 2026).

In addition to using species richness, we evaluated the main trends in biodiversity by calculating estimated mean standing diversity (Nstand; Foote 2000) (Table 1). The Nstand of each time interval, irrespective of its duration, is calculated as:

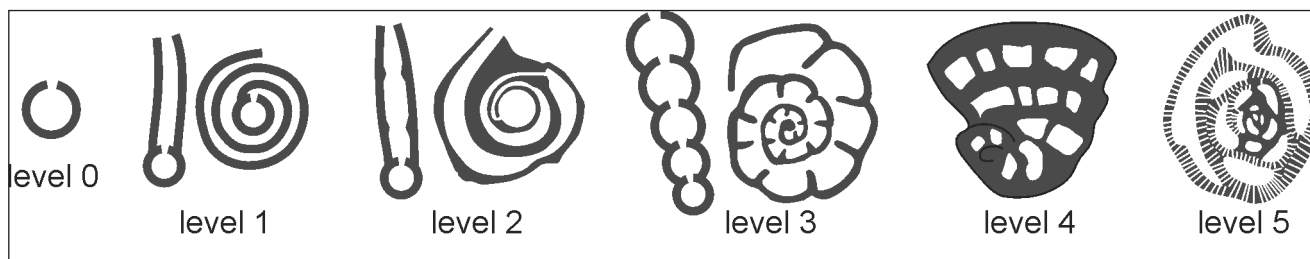


Fig. 2 - Complexity levels in foraminifera. Level 0: unilocular foraminifera; level 1: bilocular foraminifera; level 2: foraminifera with rudimentary septa; level 3: foraminifera with fully formed septa, but lacking endo- and exoskeleton; level 4: foraminifera with endoskeleton; level 5: foraminifera with exoskeleton. In case of Triassic foraminifera, the exoskeleton is represented by coarse, straight or anastomosing perforations.

$$N_{\text{stand}} = ((N_b + N_t)) / 2$$

where N_b denotes the total number of bottom-boundary crossing species, and N_t the total number of top-boundary crossing species (Foote 2000). N_b comprises the number of only the bottom boundary-crossing species (N_{b1}) and the number of the range-through species (N_{bt}). N_t is the sum of the N_{b1} and only the top boundary-crossing species (N_{t1}) (Table 1).

Origination and extinction were expressed as estimated per-capita origination rate p , and estimated per-capita extinction rate q (Foote 2000):

$$p = (-\ln(N_{bt}/N_t)) / \Delta t, \text{ and}$$

$$q = (-\ln(N_{bt}/N_b)) / \Delta t$$

where Δt represents the length of the time interval in Myr. The duration of time intervals was taken from Cohen et al. (2025). Turnover rate was calculated as the sum of p and q (Nowak et al. 2019).

Size of Foraminifera

The maximum linear dimension was taken as a fair approximation to the biovolume (Payne et al. 2011; Rego et al. 2012). This approach was advantageous in obtaining sizes for foraminifera that are known from thin sections only and/or are geometrically complex (e.g. *Cucurbita*). However, it also means that we inevitably compared very different body shapes (geometrical bodies, e.g. rods with spheres). Despite this concern, there is no correlation between the geometry of the test and its size, and the same general trend was obtained also at the family level. When the size of the specimens was not reported in the original publication, we measu-

red it from the images provided. The same size of the species was assumed for its entire stratigraphic range, unless reported otherwise. Subsequently, our database does not indicate potential changes in size within each species (see Rego et al. 2012).

Sizes of foraminifera were plotted for the entire dataset, and separately for taxa with agglutinated, combined porcelaneous and “microgranular”, and hyaline walls. Even though the type of the wall is no longer considered to be a synapomorphy (Pawlowski et al. 2013; Mikhalevich 2014; Rigaud & Martini 2016; Vachard 2016; Altın et al. 2021; Vachard & Le Coze 2024), it was still considered worthwhile to check if any separation in the data is present based on this criterion. Boxplots of logarithmic size values were created using Past statistics software v. 4.03 (Hammer & Harper 2001).

Complexity of Foraminifera

To check for possible trends in the complexity of foraminifera, we classified each species according to its architecture (Fig. 2). Unilocular foraminifera are considered the least complex and were attributed to complexity level 0. Bilocular foraminifera were assigned to complexity level 1. Complexity level 2 represents foraminifera with rudimentary septa (e.g. *Ophthalmidium*), since the introduction of septa is a step towards a compartmentalized test. Foraminifera with fully formed septa were assigned to complexity level 3. Foraminifera with additional endoskeletal structures (pillars) represent complexity level 4. Foraminifera with a thick, porcelaneous wall and a reticular inner structure or perforations were assigned to complexity level 5. This level also comprises *Aulosina* and *Involutina*, which possess large perforations and, respectively, canals (Rigaud et al. 2013, 2015). We note that the shape of the test is

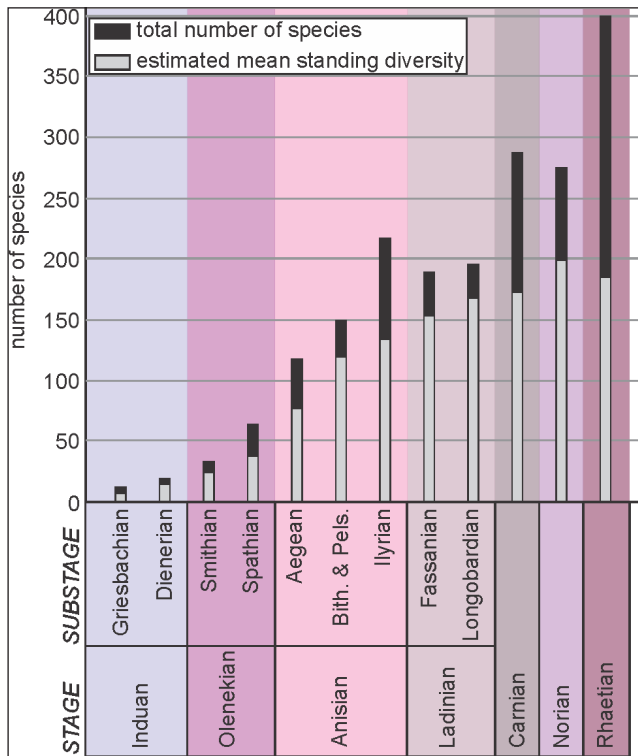


Fig. 3 - Trends in foraminiferal species diversity through the Triassic. Black columns show diversity as the raw number of species counts (total diversity). Grey columns show estimated mean standing diversity. Note the discrepancy between the two methods.

related to the microhabitat and feeding strategy of the species (Kitazato 1984; Corliss 1985; Jones & Charnock 1985; Murray et al. 2011; Setoyama et al. 2017) and does not express a degree of complexity.

RESULTS

Biodiversity

The total number of genera and species, and the Nstand at the substage level are shown in Table 1 and in Figure 3. The number of foraminiferal spe-

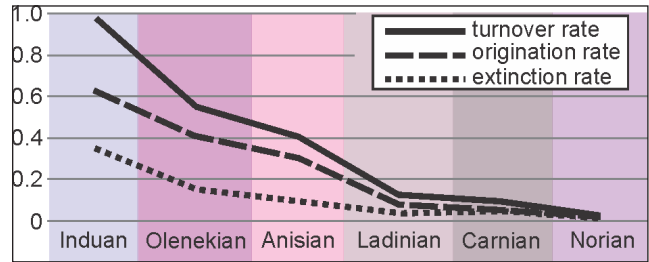


Fig. 4 - Origination, extinction, and turnover rates in foraminifera during the Triassic. The values for the Rhaetian were not calculated as Jurassic fauna was omitted from the database.

cies and genera was lowest immediately following the Permian/Triassic boundary. Total diversity shows a continued increase in the number of species until the late Anisian (Ilyrian). The number of foraminiferal species then falls slightly and remains constant in the Ladinian. We see another increase in the number of species in the Carnian, and again in the Rhaetian. The high number of species in the Rhaetian, however, is in part on account of including the detailed work of Kristan-Tollmann (1964), which describes as many as 245 species from marls of the Zlambach Formation from the Northern Calcareous Alps in Austria. In contrast, the Nstand shows a continued increase until the end of the Triassic, but at a diminished rate from the late Anisian onwards.

Origination, extinction and survival rates are shown in Table 2 and Figure 4. Values for the Rhaetian were not calculated because we were not able to determine accurate Nbt numbers because data from the Jurassic were not included in the analyzed dataset.

Origination, extinction, and turnover rates decline from the Induan to the Norian. During the Early Triassic and the Anisian the origination rate remains high above the extinction rate. A much lar-

Stage	Duration (Myr)	No. species	Ne	No	No. species per Myr	Nbt	NFt	NBl	Nt	Nb	q	p	Turnover rate (q+p)
Induan	2	24	4	20	12	4	10	4	14	8	0.347	0.626	0.973
Olenekian	3.2	73	27	53	22.8	13	34	8	47	21	0.149	0.402	0.551
Anisian	5.2	244	107	197	46.9	28	108	19	136	47	0.099	0.304	0.403
Ladinian	4.5	213	47	77	47.3	113	53	23	166	136	0.041	0.085	0.126
Carnian	9.7	297	116	131	30.6	108	72	57	180	165	0.044	0.053	0.097
Norian	21.6	272	55	91	12.6	146	71	35	217	181	0.009	0.018	0.027

Tab. 2 - Origination and extinction rates for foraminifera during the Triassic. Ne: number of extinct species; No: number of originating species; Nbt: number of range-through species; NFt: number of only top boundary-crossing species; NBl: number of only bottom boundary-crossing species; Nt: number of top boundary-crossing species; Nb: number of bottom boundary-crossing species; q: estimated per-capita rate of extinction; p: estimated per-capita rate of origination. Durations of ages are taken from Cohen et al. (2025). Rhaetian values were not calculated because data for the Jurassic was not included in the study.

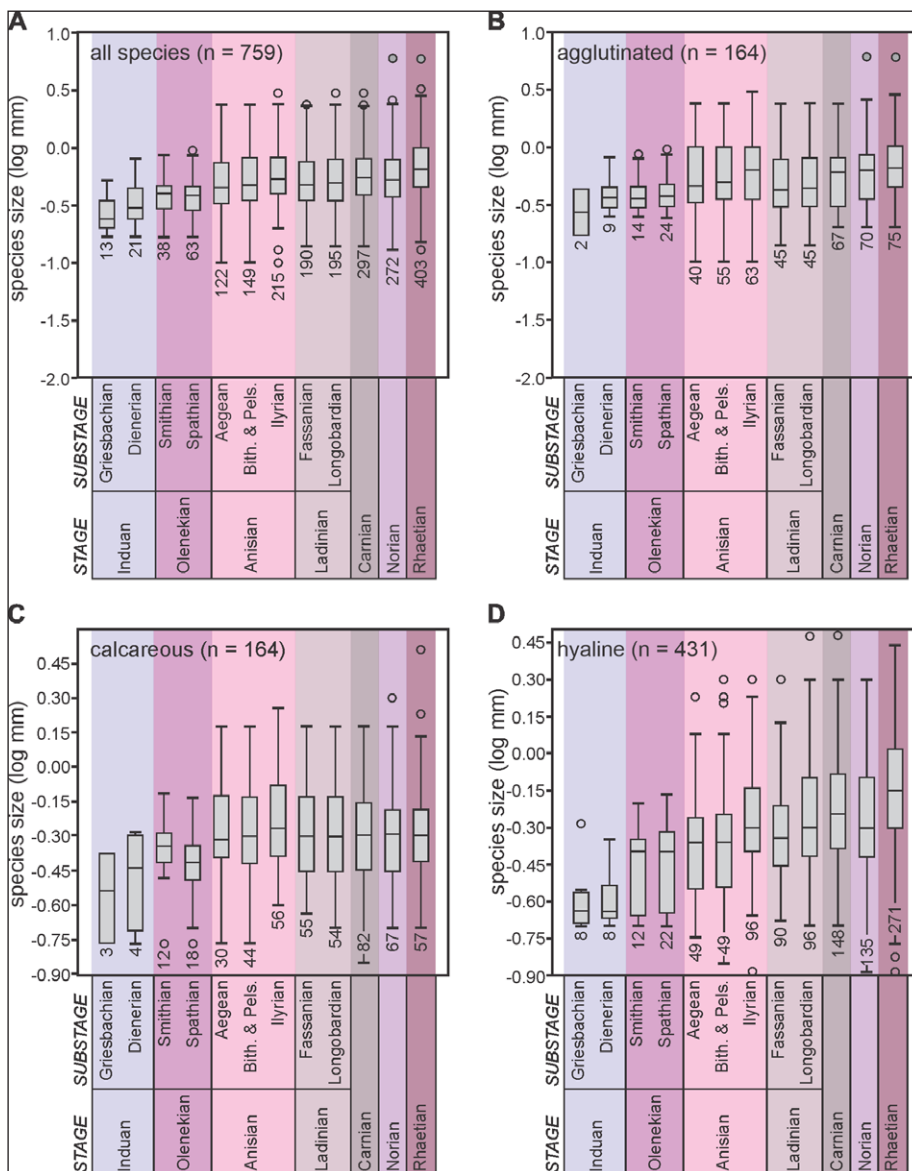


Fig. 5 - Distribution of foraminiferal sizes during the Triassic. A, All species. B, Data for agglutinated foraminifera only. C, Size of foraminifera with porcelainous and dubiously microgranular wall. D, Sizes of foraminifera with aragonitic or calcitic hyaline wall. Each boxplot displays the 25th percentile, the 75th percentile, and the median. Whiskers extend to the 5th and the 95th percentile. Circles indicate outliers. The two grey circles in the top right-hand corner of the figures A and B show position of *Alpinophragmium perforatum*, the largest Triassic foraminiferal species. The numbers next to the boxplot show the number of species in each time interval (substage or stage; see also Table 1).

ger drop in the origination rate is then recorded for the Ladinian. From the Ladinian to the Norian, the origination and extinction rates are largely the same, with the former only slightly exceeding the latter.

Size Patterns

Sizes of foraminifera were plotted to observe their distribution through time (Fig. 5). Figure 5A shows the entire dataset (759 foraminiferal species). Subsequent Figures 5B, 5C, and 5D show data separately for species with agglutinated (164 species), calcareous (164), and hyaline (431) walls, respectively. The largest, more than twofold increase of the upper size limit occurs between the Spathian (end of Early Triassic) and the Aegian (the first substage of the Anisian) (Table 3). The upper size limit remains constant from the Anisian to the end of the

Triassic. However, if we also consider the outliers, the largest species of the Triassic is the Norian–Rhaetian species *Alpinophragmium perforatum* Flügel, which can attain a size of up to 6 mm (see grey circles in the top right-hand corner of the Figures 5A and 5B). In contrast to the upper size limit, the lower size limit of foraminifera remains nearly constant, i.e. the minimum size of foraminifera does not increase through time. The same trend of increasing upper size limit and stability of the lower size limit can be seen in separate data entries for agglutinated, calcareous, and hyaline taxa (Figs. 5B–5D).

The average size of foraminifera per time interval increases until the late Anisian (Table 3). Afterwards, the average size shows only minor fluctuations, except perhaps in the Rhaetian, when it increases somewhat more significantly. The avera-

Stage	Substage	No. species	Min size (mm)	Max size (mm)	Average size (mm)	% of species larger than Triassic average (0.74 mm)	% of species larger than the average size for previous time interval
Induan	Griesbachian	13	0.17	0.52	0.28	0	(no data)
	Dienerian	21	0.17	0.81	0.34	4.8	57.1
Olenekian	Smithian	38	0.17	0.86	0.42	7.9	63.2
	Spathian	63	0.17	0.95	0.41	4.8	39.1
Anisian	Aegean	122	0.1	2.4	0.60	22.1	59.6
	Bithynian & Pelsonian	149	0.1	2.4	0.66	28.2	38.9
	Ilyrian	215	0.1	3.0	0.71	32.6	27.0
Ladinian	Fassanian	190	0.14	2.4	0.61	25.3	27.3
	Longobardian	195	0.14	3.0	0.65	28.7	36.9
Carnian		297	0.14	3.0	0.68	31.3	36.7
Norian		272	0.13	6.0	0.66	27.9	32.4
Rhaetian		403	0.13	6.0	0.80	43.2	47.9

Tab. 3 - Sizes of the smallest and the largest foraminifera per time interval, average size per time interval, and share of species larger than Triassic average and average size from the previous time interval. Average size for Triassic (0.74 mm) was calculated from the entire data set.

ge foraminiferal size for the entire Triassic is 0.74 mm, which is much closer to the lower size limit of foraminifera. Figure 6A shows how many foraminiferal species of each time interval surpass the average Triassic foraminiferal size: the proportion of species larger than the long-term average generally increases, but not at a constant rate. The highest increases in the percentage of above-average sizes happen in the early Anisian and Rhaetian. The percentage of species that are larger than the average foraminifera from the preceding interval shows a more fluctuating pattern. This value is intended to show how widespread among foraminifera is the size increase. The appearance of a single larger species will not contribute much to this value, but the appearance of larger species in numerous lineages will. A positive trend in the line thus indicates exploitation of new ecological niches and/or a general improvement in living conditions for foraminifera, whereas a negative trend indicates evolutionary stasis. Figure 6 B shows that the line stays above 0% from the Dienerian to the end of the Triassic, which agrees with the general increase in foraminiferal size (Fig. 5) and the above-average size (Fig. 6A). Furthermore, the largest increases from the average size of the preceding interval are visible for the Dienerian, Smithian, and early Anisian (approximately 60%), followed by Rhaetian (almost 48%) (Table 3; Fig. 6B).

Trends in Complexity

Figure 7 shows the distribution of levels of complexity for Triassic foraminifera for the entire dataset (Supplementary Table S2). Note that some species from Salaj et al. (1983) were reinterpreted. The species identified as *Cribratina texana* Conrad,

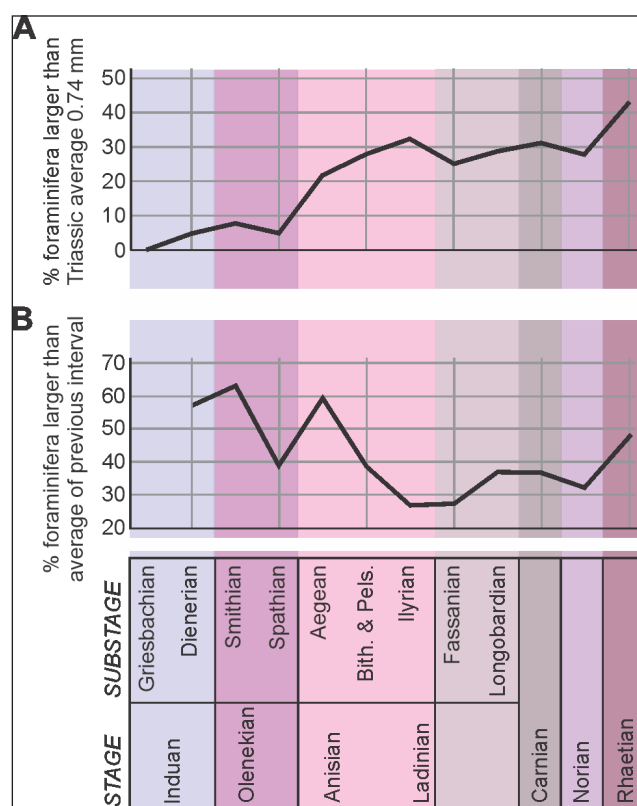


Fig. 6 - Trends in foraminiferal size increase. **A**, Share of foraminifera larger than the Triassic average of 0.74 mm. **B**, Share of foraminifera larger than the average size of foraminifera from the preceding time interval (substage or stage).

1857 in Salaj et al. (1983) is interpreted as a *Ammonobaculites* with a partly broken part of the wall. *Mesendothyra isjumi* Dain, 1958 in Salaj et al. (1983) is interpreted as an endothyroid (*Endoteba* or *Endotriada*) in the transverse section. The details of the wall of *Spiroplectammina spiralis* in Salaj et al. (1983) are not visible. *Labyrinthina* in Salaj et al. (1983) has no stratigraphic connection to *Labyrinthina* from the Jurassic and probably belongs to a different genus.

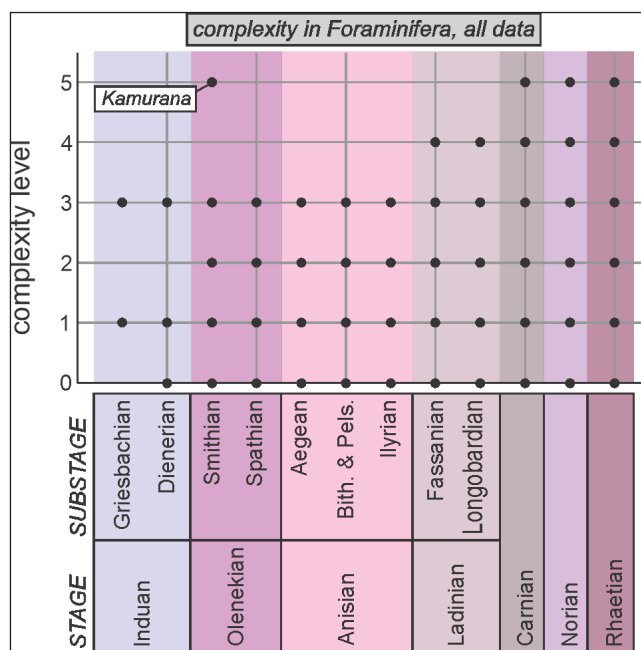


Fig. 7 - Trends in foraminiferal complexity through the Triassic. Whereas the earliest Triassic foraminifera show a relatively high level of complexity (multilocular forms with fully formed septa), the first new forms with endoskeletal features (pillars and sort of channel structures) appeared in the Ladinian, much later than the early Anisian recovery. Several genera with an exoskeleton evolved in the Late Triassic. In the present species of foraminifera, complex endo- and exoskeleton usually associate with the presence of symbiotic algae within foraminiferal tests. *Kamurana* with perforated porcelaneous wall (complexity level 5) represents a Permian survivor of a morphologically complex genus. However, Triassic *Kamurana* is smaller in size than its Permian antecedent and was not found outside Bulgaria.

The lowest recorded level of complexity was 0 (unilocular foraminifera). These simplest foraminifera were recorded from every time interval, except for the Griesbachian. The highest level of complexity in the Griesbachian was 3. Multilocular species from this interval belong to lagenids *Fronidina*, *Globivalvulina*, *Lingulina*, and *Nodosaria*. Foraminifera with agglutinated (*Pilammina*, *Glomospirella*) or porcelaneous walls (*Citaella*, *Postcladella*) from this interval only reach complexity level 1. Aragonitic *Krikoumbilica* is the first genus outside Lagenida that reaches complexity level 3 during the Dienerian. The first multilocular agglutinated foraminifera were recorded in the Smithian (*Placopsilina*, *Verneuilinoides*), and first multilocular miliolids in the Aegean (early Anisian).

Complexity did not exceed level 3 until the beginning of the Ladinian. A notable exception is *Kamurana* recorded from the Campillian beds in Bulgaria (Trifonova 1984; Trifonova & Ivanova 2001),

which has been assigned to a complexity level 5 due to perforations in the porcelaneous wall. Apart from *Kamurana*, complexity increases to level 4 only during the Ladinian. This level is first reached by *Paratriasina jiangyouensis* He, 1980 in the Fassanian, and then by *Pragsoconulus robustus* Oberhauser, 1963 in the Longobardian. *Paratriasina* is characterised by the presence of pillars (Loeblich & Tappan 1988; Zaninetti et al. 1991), while *Pragsoconulus* has some sort of canal system (Oberhauser 1963; Vettorel 1988; di Bari et al. 1997; di Bari & Laghi 1998; Rigaud et al. 2015).

During the Carnian, several genera of complexity level 5 appear for the first time: these are *Miliolipora*, *Ophthalmipora*, *Decapoolina*, *Galeanella*, *Siphonophora*, *Bispiranella* (incl. *Orthotrinacria*), *Cucurbita*, *Spiriamphorella* (in Gale et al. 2012 treated as a synonym of *Cucurbita*), and *Urnulinella* (in Gale et al. 2012 treated as a synonym of *Cucurbita*). All of these genera have thick porcelaneous walls with simple or anastomosing coarse perforations (Kristan 1957; Zaninetti & Brönnimann 1972; Brönnimann et al. 1973; Zaninetti & Altiner 1982; Zaninetti et al. 1982a, b; Salaj et al. 1983; Zaninetti et al. 1985; Senowbari-Daryan & Zaninetti 1986; Loeblich & Tappan 1988; Zaninetti & Martini 1993; Senowbari-Daryan & Flügel 1996; Gale et al. 2012, 2013).

In the Norian and Rhaetian, complexity level 5 is also reached by *Altinerina*, *Costifera* (in Gale et al. 2012 treated as a synonym of *Cucurbita*) and *Siculocosta* (in Gale et al. 2012 treated as a synonym of *Cucurbita*), all of which also belong to porcelaneous milioliporids (Zaninetti et al. 1984), but also *Aulosina* and *Involutina*, which have aragonitic hyaline walls and belong to the family Involutinidae. *Aulosina* has inner lateral wall thickenings (not yet full pillars) and coarse perforations in the wall (Rigaud et al. 2013). Besides the presence of canals crossing the outer wall, *Involutina* is also characterised by the presence of papillae in the axial region, which were interpreted as structures for catching light, and by the presence of possible rudimentary egg-holders (Rigaud et al. 2015). Genera *Kaeveria*, *Septalingulina*, and *Triasina*, which also see their first appearance in the Norian and/or Rhaetian, are characterised by the presence of pillars (see Loeblich & Tappan 1988), but appear to have simple walls, and thus represent complexity level 4. While *Kaeveria* has an agglutinated wall, the other two genera have calcitic and aragonitic hyaline walls, respectively. The complexity

of agglutinated “*Labyrinthina*” *falsomirabilis* Salaj et al., 1983 from the uppermost Norian or lowermost Rhaetian of the Carpathians (Salaj et al. 1983) is 4 or 5, since the details of the wall are not shown in the original description.

DISCUSSION

Quality of Data

The data presented in this study originates from several literature sources and the number of compiled species exceeds that of some of the previous works. For example, the study by Rego et al. (2012) encompassed 581 species and 199 genera, with data collected from 25 literature sources, compared to our 759 species from 183 genera and 106 literature sources (Supplementary Tables S1 and S2). Márquez (2005) includes 228 species from 121 genera in the analysis but selected only species with well-established stratigraphic ranges.

The data used in this study is nevertheless relatively robust, as it lacks the finer stratigraphic resolution of a logged stratigraphic succession or section, and omits the smallest and taxonomically poorly defined specimens that would perhaps be noted in a more detailed biostratigraphic study.

The number of taxa correlates with the number of references, which is not surprising because the literature selection is biased towards the works where new species were described. Thus, the number of references follows the biodiversity pattern, not the other way around. The literature sources used are paleogeographically biased: 76% of the references describe foraminiferal faunas from the western Tethys, 22% of the sources represent eastern Tethys faunas, and only 2% of the sources are for the Panthalassa Ocean. Also, almost all data comes from the (sub)tropical areas, while the higher-latitude faunas are more poorly known (e.g., Gale et al. 2020, 2021). This is due in part to historical reasons, as a lot of prominent and productive specialists in Triassic foraminifera and Triassic carbonate platforms worked at research institutes in Europe, due to the abundance of Triassic carbonates in the peri-Mediterranean area, and the accessibility of successions for study.

Despite this paleogeographic bias, the majority of the foraminiferal species had wide distribution during the Triassic (Kristan-Tollmann 1983, 1988,

1991). Even though some authors proposed the subdivision of global foraminiferal faunas into several Triassic bioprovinces (BouDagher-Fadel 2008; Chablais et al. 2011), it seems that only a few taxa were endemic.

Biodiversity of Triassic Foraminifera

The long-term Triassic evolution of foraminiferal diversity was previously studied by Tappan and Loeblich (1988), Márquez and Trifonova (2000), Groves and Altiner (2005), Márquez (2005), Groves et al. (2005), BouDagher-Fadel (2008), and Payne et al. (2011). Studies agree on a major loss in diversity at the transition from the Permian to the Early Triassic, followed by low-diversity faunas in the Early Triassic, late Early Triassic (Márquez 2005) or Anisian recovery (Groves & Altiner 2005; Groves et al. 2005; BouDagher-Fadel 2008; Payne et al. 2011). Beyond that, previous studies are not so in agreement. Tappan and Loeblich (1988) show that the number of genera continues to increase, slightly in the Ladinian, but rapidly during the Late Triassic. On the other hand, Márquez and Trifonova (2000), and Márquez (2005) calculated a slight net decrease in speciation in foraminifera from the western Neotethys area for the Carnian and Norian, and a more substantial net decrease for the Rhaetian. They also identified extinctions in the early Anisian, late Anisian, at the Carnian/Norian boundary, and in the Rhaetian. BouDagher-Fadel (2008) also suggested minor extinction events at the end of the Anisian and from the Ladinian to the Carnian, followed by an increase in biodiversity in the Norian. She also proposed a gradual decrease in foraminiferal diversity during the Rhaetian.

Due to excessively low stratigraphic resolution and compilation of data from different parts of the world, our data does not show any fine-scale fluctuations in biodiversity that resulted from repetitive environmental perturbations in the Early Triassic (Woods et al. 1999; Wignall & Twitchett 2002; Payne et al. 2004; Groves & Altiner 2005; Tong et al. 2007; Retallack et al. 2011; Chen & Benton 2012), nor the impact of the mid-Carnian environmental perturbations on foraminifera (Li et al. 2025). According to this study, mean standing diversity almost continuously increases during the Triassic (Fig. 3). Surprisingly, the highest origination rates were calculated for the Induan (Fig. 4). Origination and extinction rates both recede during the

later substages but retain constant difference up to the Anisian (Fig. 4). The rate of increase in biodiversity slows down after the middle Anisian, such that it nearly levels off in the Longobardian and the Late Triassic, if not for a slightly more pronounced increase in the Norian (Fig. 3). The inflection in the Nstand curve in the late Anisian is explained by the decrease in the origination rate which greatly exceeds the decrease in the extinction rate (Fig. 4).

Trends in Size

Our data on foraminiferal sizes show a general increase in the upper size limit from the Induan to the Rhaetian, and a slight decrease in the lower size limit (Fig. 5; Table 3; see also Rego et al. 2012). The latter, however, can instead be seen as remaining unchanged, as the smallest forms are likely to be neglected in thin sections. The overall reduction in size of foraminifera at the Permian/Triassic boundary, followed by a progressive increase in size towards the Middle Triassic has been well-documented by previous studies and attributed to reduced oxygen levels, ocean acidification, warming sea water, reduced food availability, and/or fewer competing species and predators (Payne et al. 2011; Song et al. 2011; Payne et al. 2012; Rego et al. 2012; Feng et al. 2020; Song et al. 2024). The same pattern of size evolution is mirrored in agglutinated, porcelaneous/microgranular, and hyaline taxa (Fig. 6B–D), so we find no delay or advantage in recovery based on wall composition.

The large increase in the upper size limit, contrasted by a much lower change in the lower size limit also characterizes marine animal evolution for the entire Phanerozoic (Jablonski 1997; Heim et al. 2015; Klompmaker et al. 2015). The increase of the upper size limit has been attributed to basic body plan and ecological life mode, and not any competitive advantages of the larger body (Heim et al. 2015; Klompmaker et al. 2015). Thus, a possible explanation for the increase in the upper size limit of foraminifera during the Anisian could be the expansion of ecological niches for the group and/or reflects release from some limiting environmental factor. According to Payne et al. (2012), the size changes best correlate with oxygen levels. The largest increase in the upper size limit in the early Anisian occurs simultaneously with the largest increase in the total number of foraminiferal species (Fig. 3). The increase in size also did not occur owing to a single new

species, as is suggested by an increase in the share of foraminifera larger than the Triassic average (Fig. 6A) and in foraminifera larger than the average of the previous interval (Fig. 6B). Leaving the outliers aside, the upper size limit and the mean (see Table 3) remain approximately stable for the rest of the period (also Payne et al. 2012; Rego et al. 2012).

The steadiness (or possible small decrease) in the lower size limit and the clustering of foraminifera sizes in the lower part of the size range may be due to certain advantages that the small body brings, such as the ability to survive in lower-oxygen conditions, which is an important factor in the longevity of foraminiferal species (Buzas-Stephens et al. 2025), or, at the macroevolutionary scale, having greater potential for adaptive evolution (Dombroskie and Aarssen 2010). For example, in contrast to larger benthic foraminifera, small species need less time to reproduce, and they can thus occupy environments that are less stable (Hallock 1985).

Evolution of Complexity

The complexity of organisms can be defined in different ways. Hinegardner and Engelberg (1983), and Adami et al. (2000) estimated complexity in metazoans by comparing the amount of DNA and the number of genes, respectively, whereas Valentine et al. (1994) expressed morphological complexity by determining the number of cell types in animals. As unicellular eukaryotes, foraminifera are almost as simple as an organism can be. However, their tests encompass a huge variety of shapes, chamber arrangements, and aperture types (Loeblich & Tappan 1964). A polyphyletic group of larger benthic foraminifera evolved even more complicated tests with additional subdivision of the chamber lumen, supports (pillars) and intricate structures within their external wall (beams, rafters, alveoles). Recent foraminifera with such structures are known to host various forms of unicellular photosymbiotic symbionts (Lee et al. 1979; Hottinger 1982; Lee 2006, 2010; Hohenegger 2011), which allows them to live in oligotrophic environments (Hallock 1988; Lee 2006; Hohenegger 2009; Lee 2010). Due to longer lifetimes in stable environments and the beneficial role of their endosymbionts in test mineralization, they often produce tests that are several millimeters, to several centimeters in size (Lee et al. 1979; Hohenegger 2011), and control cytoplasmic activity through hundreds of nuclei (Lee et al. 1979).

Previous studies indicate that architecturally complex Permian foraminifera suffered more drastic losses than smaller taxa (Brazier 1988; Yang et al. 2004; Groves & Altiner 2005; Song et al. 2009). The exception is the genus *Kamurana*, which seems to have a very localized appearance in the Early Triassic (Trifonova 1984; Trifonova & Ivanova 2001). Groves and Altiner (2005: p. 428) interpreted Triassic *Kamurana* as a “failed crisis progenitor”, but it could instead be called a “dead clade walking”, since the lineage seems to survive the extinction locally, but went extinct soon after (Jablonski 2002; Barnes et al. 2021). Apart from *Kamurana*, which inherited its characters from its Permian stock, our results confirm that up until the Ladinian, foraminifera only reach complexity level 3 (multilocular foraminifera without additional structural elements and with a simple wall). Interestingly, the earliest Triassic foraminifera with this level of complexity belong to the order Lagenida, which was among the most diverse foraminiferal groups in the Permian (e.g. Groves et al. 2005, 2007; Song et al. 2007). *Fronidina*, *Globivalvulina*, *Lingulina*, and *Nodosaria* all represent survivors of the Permian/Triassic extinction, like *Kamurana* inheriting features from their Permian relatives. We suspect that the absence of multilocular agglutinated and porcelaneous foraminifera from the lowermost Triassic may be due to their relative smaller numbers in the late Palaeozoic assemblages and survival in smaller and/or less dense populations.

During the Ladinian and Carnian, the highest level of complexity attained rises to levels 4 and 5, respectively. The additional internal structural elements in foraminifera serve to increase the strength of the test (Lee et al. 1979; Hallock 1988; Hohenegger 2009), and their acquisition could in principle allow some lineages to expand into environments with higher water energy. According to Rigaud et al. (2012), the development in additional inner structures represents a step towards the evolution of symbiont-bearing benthic foraminifera. However, structural changes in the walls of Triassic foraminifera do not occur in the lineages that previously acquired additional endoskeletal structures but instead characterize foraminifera with thick porcelaneous walls. Genera *Miliolipora*, *Ophthalmipora*, *Decapoalina*, *Galeanella*, *Siphonophera*, *Bispiranella* and *Cucurbita* sensu Gale et al. (2012) are characteristically found within the reef zone of Upper Triassic carbonate platforms, and it appears that their thick wall rep-

resents an adaptation to turbulent environments at the break of the platform, which represents an alternative solution to coping with high-energy waters rather than developing additional endoskeletal structures. Coarse perforations in the wall of the milioliporids and in *Siphonophera* might give the porcelaneous wall the additional transparency necessary to acquire light by the possible photosynthetic endosymbiont housed within the test, which is analogous to the recent *Peneroplis* (Hohenegger 2011). Alternatively, perforations in the wall could serve easier exchange of gas with the ambient water.

During the Rhaetian, perforations occur also in the hyaline *Aulosina* and *Involutina*. Both have previously been interpreted as housing symbionts (Rigaud et al. 2013, 2015). Several other Norian and/or Rhaetian genera from the platform-top (*Kaeveria*, *Septalingulina*, *Triasina*, “*Labyrinthina*”) are characterized by pillars, indicating an independent trend towards acquiring structures characterizing modern symbiont-bearing foraminifera. This wholesome macroevolutionary trend towards symbiotic relationships with microalgae could be related to long-term stability of the environment, during which these evolutionary steps could occur, or some new circumstance that allowed for the appearance of symbiont-bearing benthic foraminifera. Present-day symbiont-bearing foraminifera are common in oligotrophic environments (Hallock 1988; Lee 2006; Hohenegger 2009), where their food is largely provided by their symbiont (Hohenegger 2009). Hallock (1988) suggests that spreading of oligotrophic conditions could be one of the driving forces towards the more common evolution of symbiont-bearing benthic foraminifera.

Starting in the late Carnian, wide carbonate platforms developed along the passive continental margins surrounding the tropical Neotethys Ocean (Mandl 2000; Golonka 2002; Gianolla et al. 2003; Caggiati et al. 2017). Reefs developed along the edges of these platforms and/or at the rims of intraplatform basins (Schäfer 1979; Schäfer & Senowbari-Daryan 1981; Flügel & Stanley 1984; Stanley 1988; Flügel 2002; Bernecker 2005) were far-removed from fluvial sources of nutrients and tended towards more oligotrophic conditions (Hallock 1988). Secondly, the timing of the appearance of complexity level 5 in Triassic foraminifera roughly coincides with the development of the symbiotic relationship between corals and dinoflagellates

(Stanley & Swart 1995; Stanley & van de Schootbrugge 2009; Frankowiak et al. 2021). We do not know which (if any) symbionts were housed by the Triassic foraminifera, but it is tempting to suggest that corals and some of the foraminifera both acquired zooxanthellae as their symbionts. Symbiotic relationships are also beneficial for dinoflagellates, because their host provides them with carbon via calcification (Hohenegger 2009). A long, nearly parallel evolution between symbiont-bearing corals and symbiont-bearing benthic foraminifera has been documented in younger periods, especially during the Cenozoic (Lee et al. 1979).

CONCLUSIONS

The collected data shows some new features in the foraminiferal macroevolution in the Triassic.

Our analysis of species diversity coincides with previous observations that biotic diversity largely recovered by the end of the Anisian. After the Anisian, the origination rate decreases and falls into balance with the rate of extinction, which results in near constancy in the number of foraminiferal species.

Our analysis of foraminiferal sizes shows that the major increase in the upper size limit for foraminifera occurs in the early Anisian. During this time, the average size of the foraminiferal species also increases. After the Anisian, the upper size limit and the average size of foraminiferal species remain approximately the same. On the other hand, the lower size limit of foraminiferal species does not increase but remains more or less constant. This suggests the expansion of foraminiferal ecological niches in the early Anisian and/or physical/biotic recovery of the ecosystems, which could support larger individuals. The constancy in the lower size limit, and the fact that the average size of the foraminiferal species lies in the lower size range of the group, suggest that small size offers advantages to most foraminiferal species.

Lastly, the analysis of the complexity of the foraminiferal tests shows that among Early Triassic and Anisian foraminiferal species, the most complex forms were those with simple linear or spiral multilocular tests. The genus *Kamurana* proves the exception, which is herein interpreted as a “dead clade walking”. The first species with endoskeletal

pillars or canal system evolved during the Ladinian. The coarsely perforated, thick porcelaneous walls in Carnian–Rhaetian milioliporids are hypothesized as a possible indicator of symbiont-bearing benthic foraminifera. The appearance of other putative symbiont-bearing benthic foraminifera in the Norian and Rhaetian could be supported by the expansion of oligotrophic conditions along the outer parts of the extensive carbonate platforms in the Late Triassic.

Data Availability Statement. The data supporting the results of this research are available as Supplementary Tables S1 and S2 online:

<https://riviste.unimi.it/index.php/RIPS/article/view/30850>

Acknowledgements: The research presented here was financially supported by the Slovenian Research and Innovation Agency (research core funding No. P1-0011 – Regional Geology). Open access was funded by the University of Ljubljana. We cordially thank anonymous reviewers for very detailed reading and constructive comments.

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